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79, footnote, line 3 from bottom, *for correct* read *correct.*

88, line 19, *for S. F. Grey* read *S. F. Gray.*

87, line 3, *for Agrostis* read *Agrostis.*

233, under the figure, *for endophytica* read *endophyticum.*

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A cytological study of some New Zealand species and varieties of *Danthonia*.

By J. W. CALDER, B.Ag., M.Sc., Canterbury Agricultural College, Lincoln,
New Zealand. (Communicated by the BOTANICAL SECRETARY.)

(With 8 Text-figures)

[Read 6 May 1937]

INTRODUCTION.

SINCE Sutton, in 1902, first drew attention to the possible interpretation of Mendel's Laws by the application of the behaviour of the chromosomes during division and during the fertilization process the study of cytology has been of great assistance to several branches of biological science. It has helped to elucidate fundamental biological principles: it has assisted the systematist to unravel complicated taxonomic problems: it has been used by the geneticist to solve some of his problems, and has provided supporting evidence of inter- and intraspecific hybridization.

Peto (1930) examined eighteen species of the genus *Agropyron*, and showed that they formed a polyploid series with a basic number of seven chromosomes. He also produced cytological evidence of interspecific hybridization which was responsible for morphological variability. Lewitsky (1931 A) drew attention to the importance of chromosome structure, i.e. shape and size as well as the 'basic number' of a polyploid series in the study of systematics. The same worker (1931 c), in discussing the results achieved in cytological work in U.S.S.R., and particularly that of Avdulov (1931), states: 'The numerical transformations of the karyotype in the Gramineæ has proved to be of two

types. The usual "polyplid" chromosome multiplication . . . a second type also of numerical modification of the karyotype in the Gramineae is that of the "basic numbers" themselves.' He also states that higher basic numbers (12–10) and small chromosomes are characteristic of the more primitive tribes, while low basic numbers of (7–5) with large chromosomes are characteristic of the more developed tribes.

Avdulov (1931), from his study of the cytology of 110 genera embracing 221 species of the family Gramineae, has cleared up a number of difficult points in the classification of the family, and has suggested some radical alterations which he has correlated with morphological and anatomical characters. In another paper Lewitsky (1931 b), discussing the 'karyotype' in systematics, concludes as follows (p. 237): 'the karyotypical characteristic is subject to the same general rule of the relativity of systematical characters as the ordinary morphological one'. Hunter (1934), investigating the cytology of thirty species representing ten genera, supports Avdulov's findings, and concludes in a similar vein, 'a karyotype cannot be exclusively applied to any particular systematic unit. We are thus brought to a recognition of the fact that cytology can no more be used as the sole basis of classification than can any single form of anatomical or morphological study. It can, however, when properly used and correctly interpreted form a very powerful tool in the hands of the systematist who is willing to correlate its facts with those derived from other branches of study'.

The results presented in this paper indicate the extent to which cytological studies may be used in the systematics of the genus *Danthonia*.

SYSTEMATICS OF THE NEW ZEALAND DANTHONIAS.

J. D. Hooker, in his 'Flora Novae-Zelandiae' (1853–5), included eight species of *Danthonia*: *D. antarctica* Hook. f.; *D. rigida* Raoul; *D. bromoides* Hook. f.; *D. Raoulii* Steud.; *D. semiannularis* R. Br.; *D. pilosa* R. Br.; *D. gracilis* Hook. f.; *D. nuda* Hook. f.

In his 'Handbook of New Zealand Flora', published in 1867, he reduced the number of species to seven. He combined *D. antarctica* var. β , *laxifolia* and *D. rigida* in *D. Cunninghamii*; reduced his *D. pilosa* and *D. gracilis* to varieties of *D. semiannularis*; and described two new species—*D. flavescens* and *D. Buchanani*.

Buchanan, in 1880, recognized eleven species. To Hooker's list he added *D. ovata* J. Buch., *D. australis* J. Buch., *D. pauciflora* R. Br., and *D. Thomsonii* (Petrie) J. Buch. He revived *D. pilosa*, giving two forms varietal rank as *D. pilosa* var. *stricta* and var. *racemosa*, and added another variety to *D. semiannularis*, namely var. *alpina*.

Cheeseman, in 1906, recognized thirteen species and four varieties. He reduced *D. flavescens* to a variety of *D. Raoulii*, and added another variety—var. *Cheesemanii* Hack. ex Cheesem.; added *D. crassiuscula* Kirk, *D. oreophila*

Petrie, *D. planifolia* Petrie, and *D. pungens* Cheeseman; included Buchanan's *D. pilosa* var. *stricta* in his conception of *D. pilosa* and Hooker's *D. semiannularis* var. *gracilis* in *D. semiannularis*; and, following Petrie, transferred *D. pauciflora* and *D. nuda* to *Triodia*. Then, in 1925, he added three of Petrie's varieties, namely *D. oreophila* var. *elata*, *D. semiannularis* var. *nigricans*, and *D. Buchananii* var. *tenuis*.

Other species and varieties have been described in the 'Transactions of the New Zealand Institute', but these have not received recognition by T. F. Cheeseman, whose arrangement of the New Zealand species is as follows:—

- I. Two outer glumes shorter than the spikelet, very rarely almost equalling it.
- 1. Culms tall, stout. Panicle large; spikelets numerous. *D. Cunninghamii*, *D. orata*, *D. bromoides*, *D. Raoulii*.
- 11. Culms shorter, 6–18 in. Panicle small, 1–3 in. long; spikelets few, 3–12 *D. crassiuscula*, *D. pungens*, *D. australis*, *D. oreophila*, *D. planifolia*.
- II. Two outer glumes longer than the spikelets *D. pilosa*, *D. semiannularis*, *D. Buchananii*, *D. nuda*.

From the alterations and additions which have been made by the different systematists it is clear that the genus presents a number of taxonomic difficulties. Cockayne and Allan (1934) have reported the occurrence of hybridization between some of the species, and this further adds to the difficulties of classification.

MATERIALS AND METHODS.

Most of the plants used in this investigation were collected from their natural habitats and transplanted to a garden at Lincoln. From these plants material for cytological study was obtained. The locality from which each species was collected, together with its chromosome number, is recorded in the table (p. 7). Root-tips were fixed in a chromic acid-formalin mixture used by Avdulov. The proportions were 10 per cent. formalin 5 parts, plus 1 per cent. chromic acid 5 parts. For pollen mother-cells several fixatives were used, Kihara's being very satisfactory. Iron-aceto-carmine and other smear methods were tried, but usually the anthers were too small and the cells too delicate for reliable examinations to be made. The smear method was used to judge the stage at which to make fixations. The material was embedded in paraffin, cut 10 μ thick, and stained with Newton's gentian-violet method. The examinations were made with a Zeiss objective $\times 90$, N.A. 1·4, and $\times 15$ eyepiece. Drawings were made with the aid of a camera lucida, Zeiss objective $\times 100$, N.A. 1·3, and eyepiece $\times 15$, giving a magnification of about 2400 at table-level.

THE CYTOLOGY OF THE SPECIES.

The genus *Danthonia* is one of the most primitive of the tribe Aveneae (Bews). Avdulov arranges the tribe into two groups—the northern group, which is

characterized by the awn being attached to the back of the flowering glume, and includes such genera as *Holcus*, *Trisetum* and *Avena*; the southern group is characterized by the awn being attached to the tip of the flowering glume, and includes such genera as *Amphibromus* and *Danthonia*. Avdulov has investigated the cytology of a number of genera of the northern group, and finds that the size and number of the chromosomes is almost constant with 'basic number' of 7 and only unimportant exceptions in the chromosome number occur. The unimportant exception he encountered was a species of *Trisetum* which had 24 somatic chromosomes. No cytological work has so far been reported for members of the southern group.

The chromosome numbers of a number of species and varieties of *Danthonia* is given in the following list:—

D. Cunninghamii.—The plants were collected at Arthurs Pass. Pollen mother-cells showed 21 bivalents at metaphase I and divisions were normal (fig. 1). Root-tip counts showed 42 somatic chromosomes. The chromosomes of this and other species and varieties were mostly long and bi-armed, and the chromosome set was similar to those figured for other genera of the Aveneae by Avdulov (fig. 2).

D. Raoulii.—Plants of this species were collected at Akaroa, and root-tips showed 42 chromosomes. Similar forms from Porter's Pass and Burke's Pass also showed 42 chromosomes.

D. Raoulii var. *rubra*.—This is a distinct variety which grows commonly in boggy situations at Arthurs Pass and in other parts of New Zealand. The leaves are reddish, narrow and involute; the panicles are very lax, and the culms being shorter than the leaves the panicles remain among the leaves. When grown at Lincoln for three years it retained the same growth-form and colour. Cytological studies cannot assist in establishing this variety, as root-tip counts show 42 chromosomes indistinguishable from those of *D. Raoulii*.

D. Raoulii var. *flavescens*.—The plants were collected at Arthurs Pass. Pollen mother-cells showed 21 bivalents at metaphase I, and divisions were regular. Root-tip counts were not obtained. A plant was collected at Arthurs Pass which appeared to be a hybrid between this variety and *D. Cunninghamii*. Cytological evidence did not support this view. Chromosome counts in pollen mother-cells showed 21 bivalents at metaphase I, and divisions were regular.

D. ovata.—This species was obtained through Mr. J. S. Thompson of Dunedin. Root-tip counts showed 42 chromosomes similar to those of the previous species.

D. crassiuscula from Arthurs Pass (fig. 3), *D. oreophila* also from Arthurs Pass, and *D. australis* from Nelson all showed 36 chromosomes in the root-tip cells.

D. pilosa.—Pollen mother-cells of this species show 24 bivalents at metaphase I; and in most plants examined divisions were regular. In one plant irregularities similar to those described by Church (1929) were observed. The



Fig 1.



Fig 2.

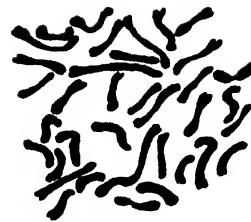


Fig 3.



Fig 4.

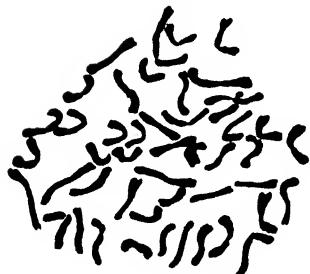


Fig 5.



Fig 6.

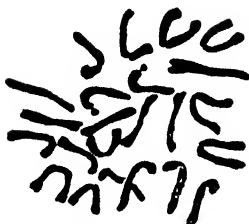


Fig 7.



Fig 8.

Fig. 1.—*D. Cunninghamii*, heterotype metaphase, 21 bivalents. $\times 2,400$.

Fig. 2.—*D. Cunninghamii*, 42 somatic chromosomes. $\times 2,400$.

Fig. 3.—*D. crassiuscula*, 36 somatic chromosomes. $\times 2,400$.

Fig. 4.—*D. semiannularis*, heterotype metaphase, 24 bivalents. $\times 2,400$.

Fig. 5.—*D. semiannularis*, 48 somatic chromosomes. $\times 2,400$.

Fig. 6.—*D. setifolia*, heterotype metaphase, 12 bivalents. $\times 2,400$.

Fig. 7.—*D. setifolia*, 24 somatic chromosomes. $\times 2,400$.

Fig. 8.—*D. Buchananii*, heterotype metaphase, 36 bivalents. $\times 2,400$.

plant appeared to be of the true *pilosa* type. Root-tip counts of five plants of *D. pilosa* showed 48 chromosomes.

D. semiannularis.—Four plants were examined, and pollen mother-cells showed 24 bivalents at metaphase I; and divisions were regular (fig. 4). These plants were typical of the lowland form of *D. semiannularis*. The chief characters which distinguish this form are the short dense panicles with from twenty to forty spikelets. Another form with a much longer panicle, fewer spikelets and much more purple coloration has been collected in montane tussock grassland at Lake Rubicon, Lake Wakatipu and Lake Pukaki. It also has 48 somatic chromosomes (fig. 5).

D. semiannularis var. *gracilis*.—This plant was given specific rank by Hooker, and is illustrated in his 'Flora Novae-Zelandiae'. Later, in his 'Handbook of the New Zealand Flora', he reduced it to a variety of *D. semiannularis*. Buchanan (1888) follows this latter arrangement of Hooker's, but Cheeseman (1906, 1925) includes this form in his interpretation of *D. semiannularis*. It grows over extensive areas in the sub-alpine vegetation at Arthurs Pass, and I have received plants from Mt. Cargill. Its most characteristic morphological characters which distinguish it from *D. semiannularis* are the dense panicles of small spikelets and the pilose nature of the back of the flowering glume. Pollen mother-cells show 12 bivalents at metaphase I, and root-tips show 24 chromosomes.

D. semiannularis var. *nigricans*.—This variety has been recorded in the Tararuas (N.I.), near Westport, and in the Lake Country. The plants examined in this study were collected on Arthurs Pass. Its needle-shaped leaves and short panicle of small spikelets distinguish it from other forms. Root-tip cells show 24 somatic chromosomes.

D. semiannularis var. *setifolia*.—This form was first described by Hooker in his 'Flora Novae-Zelandiae'. It was later described by Buchanan as var. *alpina*.

Cheeseman (1925) reverted to Hooker's name, while Cockayne (1921) claims specific rank for it. The form is widespread in alpine situations. The plants examined were collected at Arthurs Pass, and pollen mother-cells show 12 bivalents at metaphase I, and root-tip cells show 24 chromosomes (figs. 6 & 7).

D. Buchanani.—Two plants from Arthurs Pass showed 36 bivalents at metaphase I (fig. 8) and an approximate count of 72 chromosomes in root-tip cells. A very small form from the mud-banks at Lake Pukaki and a form from Mt. Torlesse also showed approximately 72 in the root-tip cells.

DISCUSSION.

The counts obtained for the different species are summarized in the table on p. 7, and are arranged in groups according to their chromosome number. Alphabetical letters have been used for the groups and sub-groups to distinguish them from those of Cheeseman, who has used numbers.

Chromosome numbers of some New Zealand species of Danthonia.

GROUP A.	n.	2n.
<i>D. Cunninghamii</i> Hook. f. Arthurs Pass	21	42
<i>D. ovata</i> J. Buch. Fiord District. J. S. Thompson.	—	42
<i>D. Raoulii</i> Steud. Akaroa, Porter's Pass, Burke's Pass ..	—	42
<i>D. Raoulii</i> var. <i>rubra</i> Cockayne. Arthurs Pass	—	42
<i>D. Raoulii</i> var. <i>flavescens</i> Hack. ex Cheeseman. Arthurs Pass	21	—

GROUP B.	n.	2n.
(a) <i>D. crassiuscula</i> Kirk. Arthurs Pass	—	36
<i>D. oreophila</i> Petrie. Arthurs Pass	—	36
<i>D. australis</i> J. Buch. Nelson	—	36
(b) <i>D. pilosa</i> Hook. f. Sumner	24	48
<i>D. semiannularis</i> Hook. f. Sumner	24	48
<i>D. semiannularis</i> , montane form	—	48
(c) <i>D. gracilis</i> Hook. f. Arthurs Pass, Mt. Cargill	12	24
<i>D. nigricans</i> (Petrie) Calder. Arthurs Pass	12	24
<i>D. setifolia</i> (Hook. f.) Calder. Arthurs Pass, Mt. Cargill ..	12	24
(d) <i>D. Buchananii</i> Hook. f. Arthurs Pass, Lake Pukaki, Mt. Torlesse	36	72?

The species in group A have 42 somatic chromosomes. Together with *D. bromoides* they are arranged by Cheeseman in the first subgroup of his group I, and form a fairly well-defined group both on morphological and cytological grounds.

The species in group B form a polypliod series with a 'basic number' of 6. The group includes those species which are arranged by Cheeseman as a subgroup of his group I. This is characterized by empty glumes shorter than the spikelet. It also includes the rest of the species which Cheeseman arranges in his group II. This is characterized by empty glumes longer than the spikelet. On a basis of chromosome numbers group B can be arranged into four sub-groups as follows :—

(a) Those with 36 chromosomes. Three species have been examined, namely *D. crassiuscula*, *D. oreophila* and *D. australis*. Together with *D. punctata* they constitute a well-defined group based on morphological characters.

(b) Those with 48 chromosomes. This sub-group includes *D. pilosa* and *D. semiannularis*. Both species are commonly found growing in the same association; and Cockayne and Allan (1934) record the existence of numerous hybrid swarms. Both species also show extensive polymorphy. A distinct form of *D. semiannularis* from the montane tussock grassland is indistinguishable cytologically from the lowland forms.

(c) Those with 24 chromosomes. This sub-group has three interesting forms which, from the cytological evidence, supported by morphological characteristics, claim specific rank. One of these, namely *D. gracilis*, is included by Cheeseman in his description of *D. semiannularis*; the other two.

namely *D. nigricans** and *D. setifolia*†, are considered to be varieties of *D. semiannularis*.

(d) The form with 72 chromosomes. *D. Buchanani* is the only species which was found to possess 72 chromosomes. It also is a polymorphic species; and Cockayne and Allan record that it hybridizes with *D. semiannularis*.

CONCLUSIONS.

The investigation has disclosed two cytological phenomena which have been shown by Avdulov and Lewitsky to be of value in systematics, namely a change in the 'basic number' and the simple polyploid multiplication of the chromosomes. The cytological studies support in some degree the systematic arrangement of the species based on morphological characters, but they give greater weight to some morphological differences, with the result that a modified arrangement can be put forward with confidence. Three forms have also been raised to specific rank.

The origin of the different 'basic numbers' is not known. Avdulov, in his investigation of the northern members of the tribe Aveneae, finds that the 'basic number' is 7, 'with unimportant exceptions'. In the New Zealand species of *Danthonia* a polyploid series with a 'basic number' of 6 occurs. *Triodia Thomsonii* Petrie, which was first described by Buchanan as *D. Thomsonii*, was also examined during this investigation, and showed 24 bivalents at metaphase I. This plant is closely related to the North Island *D. nuda*, and is distinguished from it by indefinite morphological characters. These facts suggest that a detailed study of the southern genera of the Aveneae may be of definite value in solving problems of relationships.

SUMMARY.

The value of cytology in systematics of the Gramineae is discussed. The cytology of thirteen New Zealand species of *Danthonia* has been investigated. Two groups with different 'basic numbers' have been found to occur—one with 42 as the somatic number and a 'basic number' of 7, the other forming a polyploid series of 24, 36, 48 and 72 somatic chromosomes and a 'basic number' of 6. A new systematic arrangement of the species based on cytological data is suggested. Three forms with 24 chromosomes which have been considered to be varieties of *D. semiannularis* have been raised to specific rank as *D. setifolia*, *D. gracilis*, and *D. nigricans*.

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† *Danthonia setifolia* (Hook. f.) Calder, comb. nov.—*D. semiannularis* var. *setifolia* Hook. f. *Fl. N.Z.* i, 304 (1853); Cheeseman, *Man. N.Z. Fl.* 891 (1906); op. cit. ed. 2, 178 (1925).

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Observations on *Himanthalia lorea* (L.) Lyngb. By DOROTHY C. GIBB, B.Sc.,
Ph.D. (Department of Botany, Aberdeen University, and Marine
Biological Station, Port Erin, Isle of Man) (Communicated by Professor
J. R. MATTHEWS, M.A., F.L.S.)

(PLATES 1 & 2 and 3 Text-figures)

[Read 21 January 1937]

HIMANTHALIA LOREA is a common component of the vegetation on the rocky shores of the British Isles. It has already been the subject of much research, but certain aspects of its life-history such as germination, egg-dispersal mechanism, and morphological variations have not been fully investigated. The observations recorded below were made partly at Cove Bay, a few miles south of Aberdeen, and partly in the Isle of Man, where the species occurs abundantly on the rocky coast at Castletown and Port St. Mary.

MORPHOLOGY.

The most detailed observations on the morphology of the plant *in situ* were made at Port St. Mary. *Himanthalia* occurs at a low level on the shore from eight feet below Mean Sea Level (i.e. one foot above low water ordinary spring tides there) to one and a half feet below Mean Sea Level. It ranges at a level about one foot higher in pools. Only comparatively few plants are present in the upper and lower limits of the zone; the densest growth occurring between one foot above low water neaps (i.e. four feet below M.S.L.) and seven feet below M.S.L. Tidal level plays an important part in determining the outward form of the plants, affecting both the vegetative thallus and the receptacles.

Vegetative thallus.

At the higher tidal levels the vegetative part of the thallus is much flattened and button-like (fig. 1 a); it has a short stalk, a well-marked basal disk, and is distinctly tougher than in plants from the lower levels. This form took from one to two years to develop at Port St. Mary before any receptacles were formed.

At the lower limits of the zone the majority of the plants have a vegetative thallus of a different shape. They are in the form of inverted cones whose

upper surface has been extended into a slight rim and the central part somewhat depressed (fig. 1 b). These did not take more than one year to develop at Port St. Mary before they gave rise to receptacles. The texture is not nearly so tough as in the button-shaped thallus at the time when the receptacles sprout.

Between the lower and upper limits of the zone, intermediate forms occur, the majority tending towards the more flattened type, but not growing nearly so large in diameter nor so tough. Receptacles appear earlier than in the characteristic button-shaped type.

Many abnormal forms have been noticed ; for example, some never develop beyond the early pear-shaped form, but grow fairly large, retain their succulent character, and give rise prematurely to receptacles (fig. 1 c). Others develop a little further until they have attained a flattened upper surface, then grow to a considerable size and give rise to receptacles very early (fig. 1 d). A few

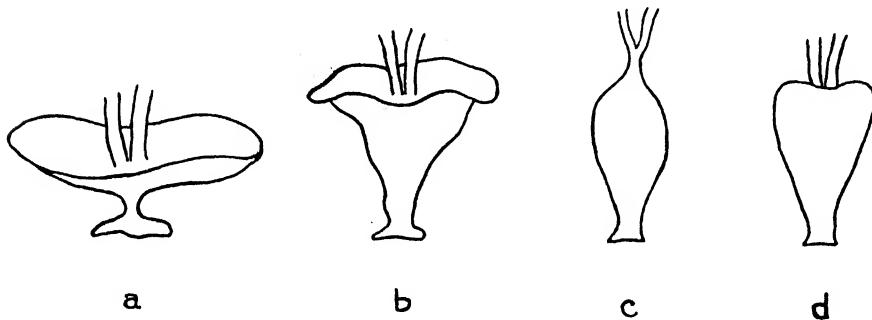


FIG. 1.—Vegetative thallus.

a, high-level form ; b, low-level form ; c, d, abnormal forms.

freak plants have also been noticed in which the vegetative thallus is divided, giving rise to more than one surface from which receptacles sprout.

Receptacles.

During July receptacles begin to appear in the form of slight swellings in the centre of the thallus ; each has a conspicuous apical pit. The number arising from each thallus varies from one to four, but two is most usual. Measurements of the developing receptacles of plants from the lowest and highest parts of the dense zone were made at Port St. Mary in 1933-4. Samples of about fifty plants from each of the two levels were measured about the middle of each month. The average length and breadth over the year is shown in fig. 2 and Table I (p. 14). Until October, when the measurements were begun, growth was very slow. The curves show clearly the great difference in length and breadth of the receptacles from the two levels, the low-level receptacles being longer and narrower than those from the higher level.

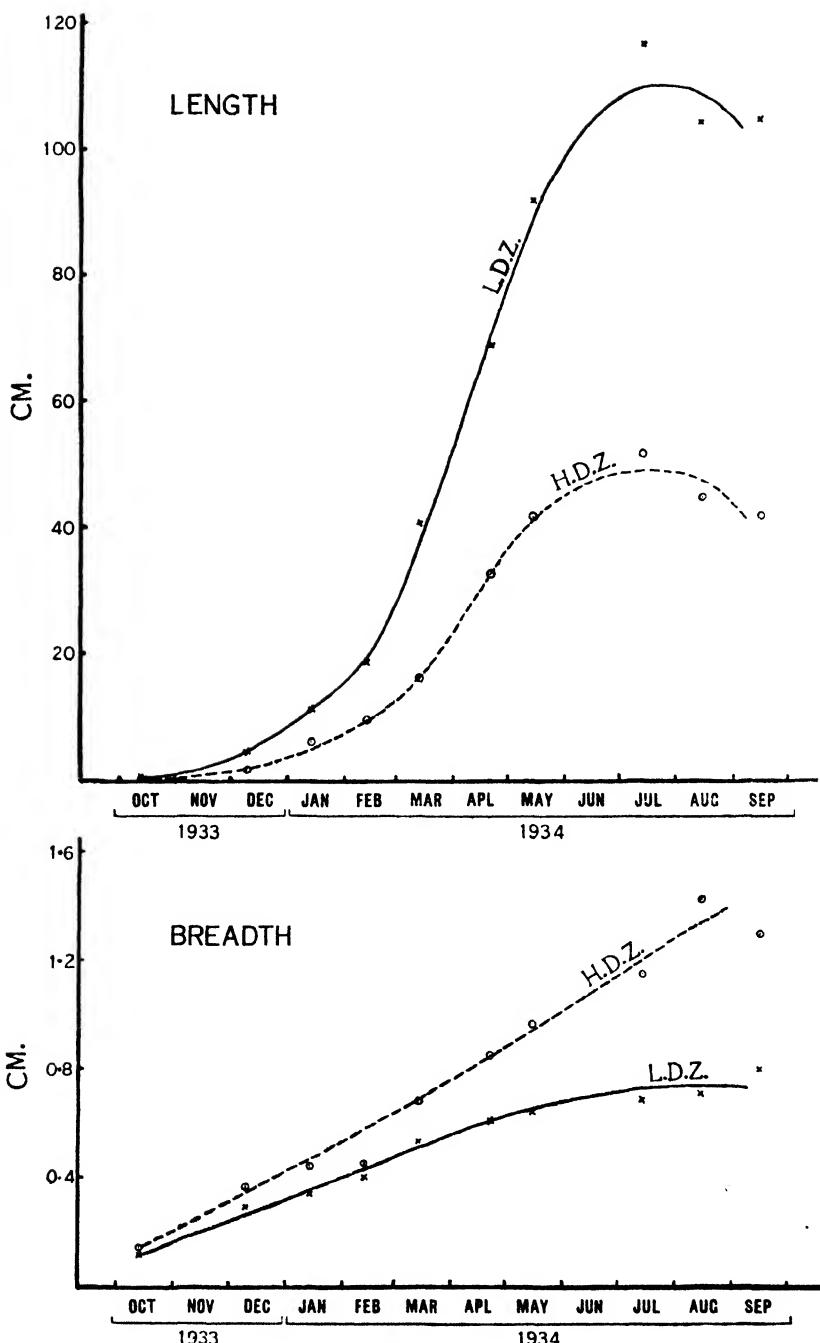


FIG. 2.—Growth-curves of the receptacles.

H.D.Z. Plants from highest part of dense zone

L.D.Z. Plants from lowest part of dense zone.

TABLE I.

	12 Oct.	9 Dec.	13 Jan.	12 Feb.	13 Mar.	21 Apr.	14 May.	13 July.	14 Aug.	15 Sept.	
H.D.Z.	Av. length .. (in cm.)	0·14	1·8	6·2	9·4	16·4	32·1	41·8	53·0	44·4	41·6
	Av. breadth .. (in cm.)	0·14	0·37	0·44	0·45	0·68	0·85	0·97	1·15	1·43	1·30
L.D.Z.	Av. length .. (in. cm.)	0·28	4·9	11·4	18·8	40·9	68·9	93·0	117·0	114·3	114·8
	Av. breadth .. (in cm.)	0·12	0·29	0·34	0·40	0·53	0·64	0·61	0·69	0·71	0·80

In fig. 3 and Table II the degree of branching of the receptacles of the measured plants from each zone is shown. At the lower level practically all the branching took place from November to January, i.e., when the receptacles were very young. At the higher level, however, the branching did not take place so soon; the higher level plants were about a month later in reaching their maximum degree of branching. In October the young receptacles had not started to branch, but by November, of the plants of the lower level, 60 per cent. had branched dichotomously once, while, of the plants at the higher level, only 10 per cent. had branched once. A similar discrepancy between the two levels was shown in December.

TABLE II.

No. of forks.	12 Oct.		12 Nov.		9 Dec.		13 Jan.		12 Feb.		13 Mar.		21 Apr.		14 May.		
	Per cent.	H.D.Z.	Per cent.	H.D.Z.	Per cent.	L.D.Z.	Per cent.	H.D.Z.	Per cent.	L.D.Z.	Per cent.	H.D.Z.	Per cent.	L.D.Z.	Per cent.	H.D.Z.	L.D.Z.
0	100	100	90	40	78	9	0	0	0	0	0	0	0	0	0	0	0
1	10	60	22	66	34	0	0	0	0	0	0	0	0	0	0
2	25	64	70	58	8	24	4	18	6	8	0
3	2	30	38	80	66	84	68	72	84	86	..
4	4	12	10	12	14	22	8	14

Branching at both levels was most rapid from December to January. At the lower level, by the middle of January, 30 per cent. had branched three times

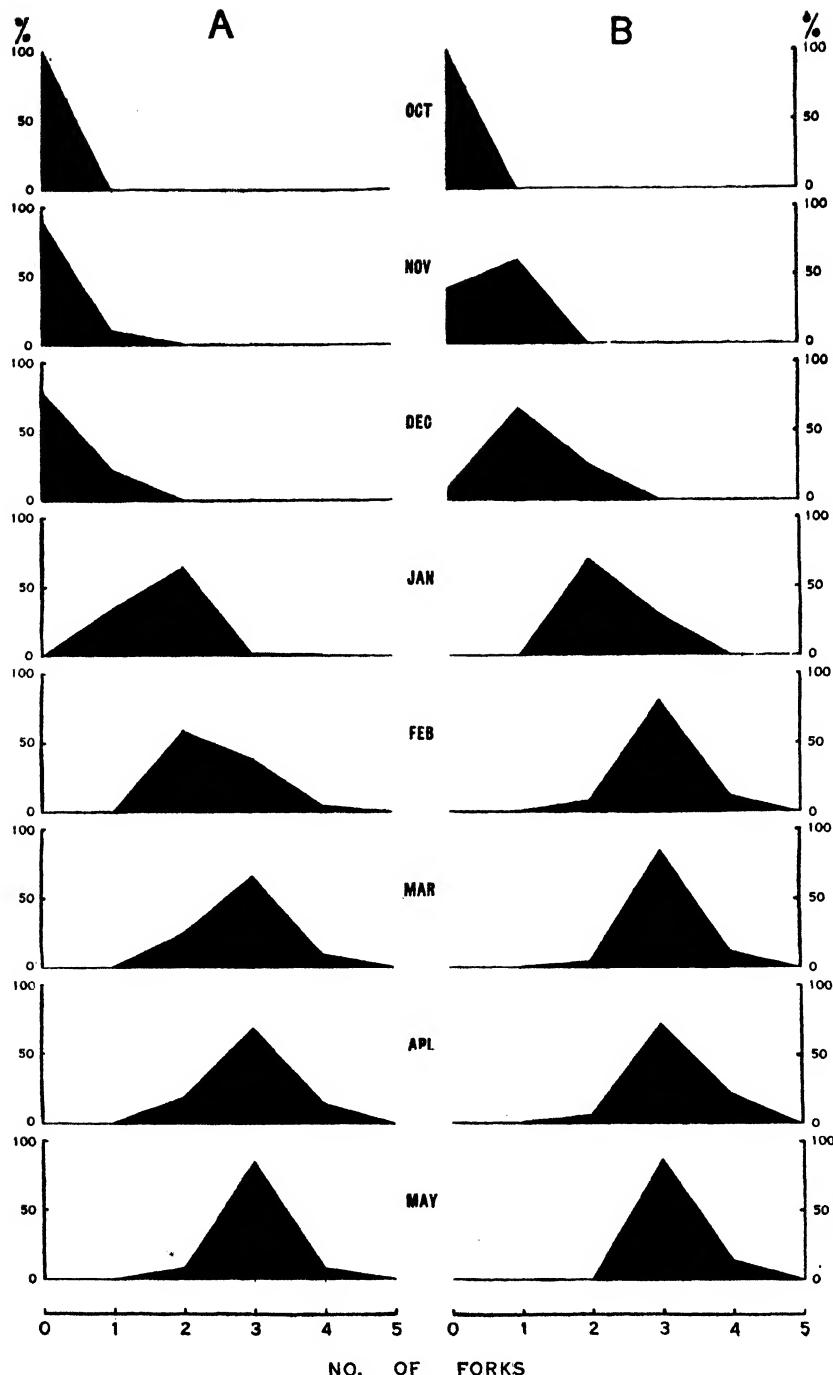


FIG. 3.—Branch-development in the receptacle.

- A. Plants from highest part of dense zone.
- B. Plants from lowest part of dense zone,

and 70 per cent. twice. At the upper level 2 per cent. had branched three times, 64 per cent. twice, and 34 per cent. once. At the lower level branching was almost at an end by February when there were 12 per cent. with four forks, 80 per cent. with three forks, and 8 per cent. with two forks. At the higher level, however, branching continued for about a month longer, and was almost stationary by March, when 10 per cent. had four forks, 66 per cent. three forks, and 24 per cent. two forks. No further branching took place, so the difference between the plants at the two levels then established was maintained.

Fig. 2 shows that the rapid increase in length began only after branching had ceased (February). This was more marked at the lower level. The breadth, however, did not seem to be influenced by branch formation, for the rate of growth remained constant. The fall in the length-curve from July onwards can be explained by the breaking away of the tips by wave action.

Though most of the receptacles do not persist after the sexual products have been shed, yet some, chiefly at the higher level, remained in a stunted and mutilated condition. The conceptacles became packed with mucilage hairs and bulged considerably. A few of these remaining plants have been seen to give rise to young receptacles during the next season, but these grew directly from the basal portion of the old one and not from the vegetative part of the thallus.

The plants have all been found to be dioecious, but there is no noticeable difference in form between the sexes.

LIBERATION OF THE SEXUAL PRODUCTS.

Periodicity.

Immersing plants in sea-water in the laboratory at the same time as they would have been covered by the tide on the shore resulted in the liberation of the sexual products. Thus, on the shore, reproduction probably takes place twice a day with the rising tide. Reproduction began in July and continued till about January ; a ripe plant continues to shed gametes for several weeks. The extrusion of gametes took place sooner and in greater quantity at the time of spring tides than at neaps. This suggests that time of exposure has a definite influence on the extrusion. Other observations, however, showed that there is also a definite tidal rhythm independent of exposure. If the plants were left exposed beyond the usual time of covering by the sea, they released their products about the same time as those which were immersed. Similarly, plants kept immersed continuously, released their products at the same time as those undergoing the normal intermittent exposure on the shore for about two days ; thereafter liberation was irregular and small in quantity.

Egg-dispersal mechanism.

The observations already made by Oltmanns (2) on the egg-dispersal mechanism of *Himanthalia* have been confirmed and extended. It is very simple as compared with other members of the Fucaceae. Oltmanns has shown

that, before liberation, each mature oogonium, containing one oosphere, is attached to a stalk-cell in the conceptacle. The oosphere is surrounded by three membranes—the exochiton, mesochiton, and endochiton. When liberation takes place the thin exochiton bursts, releasing the oosphere with its two remaining membranes into the conceptacle cavity. My own observations have shown that the oospheres are then extruded in groups through the ostiole. The exact mechanism of this ejection is not clear. It may perhaps be due to pressure set up by intake of water following a shrinkage caused by differential drying during the preceding period of exposure. This view is supported by the fact that the interval before release, when receptacles are immersed, is shorter, and the evacuation more thorough, following the longer exposures at spring tides, than it is after shorter exposures at neap tides.

Once free from the ostiole and in contact with sea-water, the membranes surrounding the oosphere immediately swell up (Pl. 1, figs. 1 & 2; cf. Oltmanns (2), pl. xv, figs. 15 & 16). I have observed that before coming into contact with sea-water the mesochiton is not distinct; after it has been in water for a few seconds, it becomes as broad as $13\text{--}15\mu$, except at the basal region where the four distinct pits shown by Oltmanns are seen. The inner membrane also swells or becomes stretched chiefly at the base near the pits and towards the apex, where it usually reaches a width of $20\text{--}40\mu$. As Oltmanns has observed, the abortive nuclei and traces of protoplasm are already visible within the inner membrane when the membranes have swollen up. All these structures show up best with gentian violet. The contents of the oosphere, which is more or less spherical ($300\text{--}500\mu$ in diameter), are very dense, and so the nucleus is not visible.

Biochemical tests on the oospheres, while they still retain their membranes, show that they contain a large quantity of fucosan. The membranes stain blue with methylene blue, and are therefore probably mucilaginous.

The escape of the oosphere from its remaining membranes is somewhat different from Oltmanns's (2) description (pl. xv, fig. 17). Immediately after the membranes have stopped swelling, the oosphere develops a protuberance, usually laterally, which abuts on the inner membrane (Pl. 1, fig. 3). A small rupture occurs through which the protoplasmic membrane passes. The fluid contents follow quickly, rushing through the narrow isthmus, the part outside enlarging quickly (Pl. 1, figs. 4, 5, & 6). It is usually only a matter of seconds before all the contents have left the membranes. The oosphere, when released, immediately regains its spherical form; the abortive nuclei can be seen within the cast-off membranes (Pl. 1, figs. 5 & 6; cf. Oltmanns, i.e. fig. 18). Occasionally during the extrusion, small pieces of oosphere become detached prematurely (Pl. 1, figs. 7 & 8).

If the oogonia after liberation from the conceptacle are left exposed to the air for some time before placing them in sea-water, only a few leave their membranes; after two hours' exposure to air practically none can escape. Thus liberation into water is essential for the further development, since it has been observed that fertilization cannot take place if the membranes are retained.

Release of the male products.

The release of the spermatozoids in *Himanthalia* is similar to that in *Fucus* as described by Oltmanns (3). Each antheridium is attached to an antheridial branch and the exochiton bursts to liberate it into the conceptacle. It is 42–60 μ long, 9–12 μ broad at the centre, and contains forty to fifty mature sperms. As soon as it comes in contact with sea-water the capsule swells at one end to a width of approximately 15 μ . Staining with methylene blue indicates the presence of mucilage. A few seconds after contact with sea-water the capsule ruptures at the end opposite to the swelling and the contents bulge through the gap. At this stage the spermatozoids may still be enclosed in a very thin membrane, the endochiton, but it is impossible to make out whether the capsule has one layer or two. At any rate the extruded mass quickly breaks up and the sperms immediately become active. Some activity is shown by the sperm while still within the capsule before rupture.

When liberated the sperms are nearly spherical and are 3–4 μ in diameter. They have an 'eye-spot' 1 μ in diameter and two cilia 10–14 μ long. The very active movement of the sperms in water lasts for a considerable time. In dilute suspension they remain active as long as twelve hours, and in heavy suspension about fifteen hours. If sperm capsules released from the conceptacles are not put in sea-water, but are allowed to remain on the outside of young receptacles exposed to the air, they remain alive for much longer; e.g., when water was added forty-eight hours later, some of the sperms were still living. Thus exposure to the air is much more detrimental to the female than it is to the male gametes.

FERTILIZATION.

When the oospheres and sperms have been released together in sea-water, the sperms cluster round the oospheres, moving actively all the time. Thuret and Bornet (4) have shown that while in *Fucus* their movement sets the eggs in motion, this does not happen in *Himanthalia*, probably because the oospheres are so much larger.

GERMINATION.

Some observations on the germination of *Himanthalia* have been made by Oltmanns (2) and, according to him, by Rostafinski. Thuret and Bornet (4) were able to rear the fertilized eggs in culture; and Farmer and Williams (1) also obtained some stages. The later development has already been described by Wille (5).

By the use of culture solutions successful germinations were achieved several times in the Isle of Man. The eggs and sperms were mixed in fresh sea-water and the eggs immediately slipped out of their membranes; no fertilization takes place unless this occurs. No nutrient salts were added to the culture until a few days had elapsed, and thereafter a little was added every ten days. The composition of the added solution was as follows:—

Magnesium sulphate, 2 gm.	dissolved in 1 litre sea-water.
Potassium nitrate, 2 gm.	
Calcium phosphate, 2 gm.	
Potassium iodide, small crystal.	
Potassium bromide, trace.	

No great difficulty was experienced in rearing the plants until about three months had elapsed, when growth became very slow or stopped. The plants had by then passed the earliest phases of germination and were clearly visible to the naked eye. Material at later stages of development could easily be collected from the shore.

Samples for examination were fixed in chromo-acetic acid consisting of 25 c.cm. 1 per cent. chromic acid, 20 c.cm. 1 per cent. acetic acid, and 45 c.cm. sea-water.

A fertilization membrane is formed during the first hour ; the sperm nucleus was not observed in the cytoplasm. Fertilized and unfertilized eggs can be distinguished on fixing when the former turn brown. A few hours after fertilization, the eggs adhered to one another probably owing to a mucilaginous secretion of the fertilization membrane. Thereafter there was noticeable thickening of the membrane. After one to two days a germ-tube was formed (Pl. 1, fig. 9). Colourless at first, it burst through the thick fertilization membrane ; and the chromatophores, granules and general cell-contents gradually streamed into it as it enlarged (Pl. 2, figs. 16 & 18). This germ-tube may attain a considerable length ; it usually showed many constrictions which gave it the appearance of being beaded, and at the tip the membrane was very thin (Pl. 1, fig. 11). At this stage the germling was uninucleate, the first division of the fusion nucleus not having been observed till two and a half days after fertilization. Treatment with vanillin and concentrated hydrochloric acid showed the presence of a large quantity of fucosan scattered in the form of granules or droplets amongst the numerous plastids ; staining the membrane with methylene blue indicated that it was probably mucilaginous.

After the fusion nucleus had divided, a syncytial stage (Pl. 1, fig. 12) followed. The occurrence, normally in *Himanthalia* and exceptionally in *Fucus*, of a syncytial stage has already been observed by Farmer and Williams (1). The nuclei divided very rapidly and the stages of cell-division were seen clearly during this phase (Pl. 1, fig. 10). The resting nucleus is large with one large nucleolus and a well-marked chromatin network. Division is intranuclear, the nuclear membrane not disappearing until late anaphase is reached. Much kinoplasm surrounds the nucleus during the early prophase when the nuclei enlarge. The number of chromosomes in the diploid condition is twenty-eight, as stated earlier by Farmer and Williams (1). Well-marked asters appear at each pole, and the chromosomes become arranged on a clearly defined spindle which is separated by a clear space from the persistent nuclear membrane. The chromosomes are large and, in early anaphase, can be easily counted.

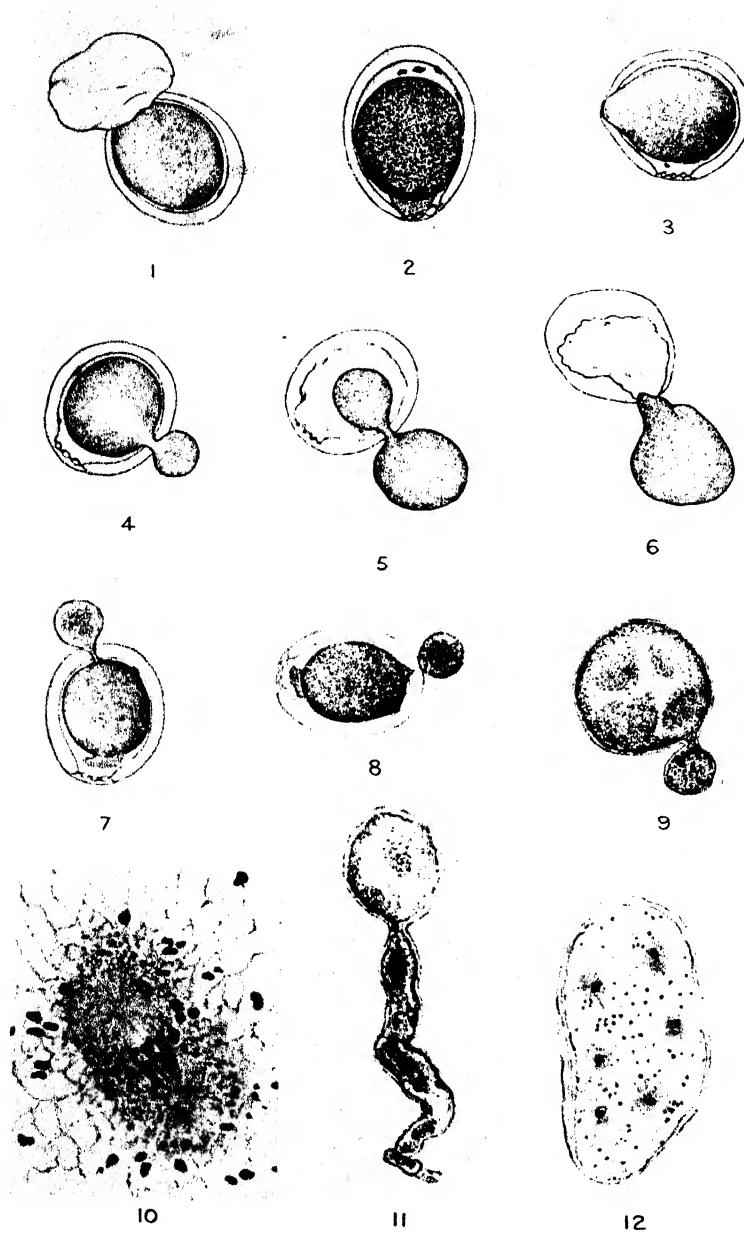
Very thin cell-walls were observed after about five days, the youngest stage with cell-walls having eight to ten cells. Each cell contained a well-marked nucleus surrounded by a dense aggregation of granules. The exact fate of the primary germ-tube is unknown. It lost in importance as the body of the germling grew in size, and possibly this primary germ-tube dwindled and shrivelled after having fulfilled its function of attaching the young germling. It did not appear to be continued as a permanent rhizoid, as rhizoids make their appearance (see below) from lower cells of the body of the germling. Rapid cell-division must take place after wall-formation has started, for, on the sixth day, stages were seen with a much greater number of smaller cells (Pl. 2, fig. 15).

By the end of the first week the plants were about 256μ in diameter and rhizoids began to develop. These arose as projections of several cells at one end (Pl. 2, fig. 17). Cross-walls were formed as the rhizoids grew longer, and in later stages the rhizoids branched slightly. The number of cells in the body of the germling had greatly increased, and the beginning of tissue-differentiation could be seen in the cells at the surface. These were smaller and had more chromatophores than the cells in the centre or in the basal region where the rhizoids were appearing.

By the end of the second week the plants were about 340μ in diameter. They consisted of a large number of small cells and their rhizoids had attained a length of 70μ . When three weeks old (Pl. 2, fig. 13) there was a distinct differentiation into an outer assimilatory layer of palisade-like cells with many chromatophores concentrated at the inner walls. The internal cells had become larger and contained relatively few chromatophores mostly arranged round the walls. The rhizoids had become much longer. The remains of the fertilization membrane were attached to the lower part of the germling close to the rhizoids. When one month old the plants were 376 – 733μ in diameter and the rhizoids 244 – 770μ long. By the end of seven weeks the beginning of the apical pit was visible.

After three months the plants had become pear-shaped and further differentiation had taken place. The cells towards the basal end were much larger than those of the upper part; the rhizoidal filaments had become very long (about 1 mm.) and somewhat branched. The plants were about 1 mm. long, apart from their rhizoids, and the apical pit was distinct. About two-thirds of each cell in the outermost layer was packed with fucosan granules, while the inner cells had only a few. There seemed to be little difference in the fucosan content during the night and during the day. When tested with methylene blue only the outer cuticle and the rhizoids indicated mucilage. Cellulose could not be detected microchemically at this stage, but Dr. Russell-Wells of University College, London, determined its presence macrochemically in samples of the mature plant sent to her for analysis.

Later stages of development could be followed only by collecting young plants from the shore; their exact age was of course unknown. The rhizoids dwindled gradually and the basal disk was formed by pseudoparenchymatous cells



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HIMANTHALIA LOREA (L.) LYNGB.



13



14



15



16



17



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(Pl. 2, fig. 14). A further differentiation then appeared in the outer assimilatory layer, which consisted of two to three layers of cells, the outermost one being palisade-like, the others being composed of large iso-diametric cells. Within these layers there was a loose network of cells and hyphae which occupied only a small part of the inner space.

SUMMARY.

(1) Morphological variations of *Himanthalia lorea* at different tidal levels on the shore are described.

(2) An account is given of the mechanism of release of the sexual products.

(3) Development from the fertilized egg to the young sporeling 1 mm. in length has been traced by cultures.

The thanks of the author are due to Professor J. R. Matthews, Dr. Margery Knight, and the staffs of the Marine Biological Stations at Port Erin and Millport for advice and help throughout the work, which was carried out during the tenure first of a Kilgour Senior Scholarship and later of a Carnegie Scholarship.

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EXPLANATION OF THE PLATES.

PLATE 1.

Fig. 1. Oosphere enclosed in meso- and endochiton (exochiton attached). $\times 33$.

Fig. 2. Oosphere before release from meso- and endochiton. $\times 33$.

Fig. 3. Oosphere with a lateral protuberance. $\times 33$.

Figs. 4-6. Stages in the escape of the oosphere from its membranes. $\times 33$.

Figs. 7-8. Premature detachment of a portion of the oosphere. $\times 33$.

Fig. 9. Germling—very early stage showing beginning of the germ-tube. $\times 35$.

Fig. 10. Section showing an early anaphase in the syncytial stage of germination. $\times 916$.

Fig. 11. Germling with long germ-tube. $\times 35$.

Fig. 12. Section through syncytial stage of germling. The nuclei are in early prophase and surrounded by kinoplasm. $\times 131$.

PLATE 2.

Fig. 13. Photomicrograph showing a section through germlings three weeks old. $\times 45$.

Fig. 14. Photomicrograph of section of germling showing formation of basal disk. $\times 37$.

Fig. 15. Photomicrograph showing section through germling five days eighteen hours old. $\times 21$.

Fig. 16. Photomicrograph of section through germlings one day fifteen hours old. $\times 56$.

Fig. 17. Photomicrograph of section through a germling one week old, showing young rhizoids. $\times 196$.

Fig. 18. Photomicrograph showing a section through a germling one day eight hours old. $\times 239$.

The light relations of *Euglena limosa* Gard.—Part I. The influence of intensity and quality of light on phototaxy. By ROSE BRACHER, Department of Botany, The University, Bristol. (Communicated by Professor MACGREGOR SKENE, D.Sc., F.L.S.)

(With 4 Text-figures)

[Read 21 January 1937]

EUGLENA LIMOSA forms a continuous green carpet on the tidal mud of the Avon at Bristol during the summer months from April to October. The organism is devoid of a flagellum, and creeps on the surface and into the mud by amoeboid movements. When the light intensity falls below a certain value the *Euglena* burrows below the surface ; at a somewhat higher intensity it comes to the surface again ; a still higher intensity is necessary for sufficient photosynthesis to take place for the formation of the carbohydrate reserve "paramylon" and the multiplication of the organism. Under ordinary intensities of daylight *Euglena* lives on the surface of the mud, but at the approach of high tide it burrows. Further, on removal from tidal influence, it shows a tidal rhythm for three days, burrowing in light at the time of day when high tide would have reached it under natural conditions. The movements which take place in nature depend, therefore, on the interaction of the factors of tide and light, and they are also affected by other factors such as temperature and the moisture content of the mud. A detailed account of these movements and their relation to the life of the organism is given in two previous papers (5 and 6). The present investigation is concerned with the effect of light intensity and wave-length on the movements of the organism. A further paper will deal with the relation of these factors to photosynthesis and reproduction.

Mainx (22) has stated that the *Euglenae* are not suitable for the experimental testing of these reactions owing to such movements as swarming caused by sudden changes in external conditions. Therefore, prior to the main investigation, I have attempted to analyse and control the behaviour due to each known external factor or to the interaction of more than one, and to search for any relation between these responses and the rhythm exhibited by the organism (p. 29).

The possibility of the existence of *constant* intensity-limits for the three processes phototaxy, photosynthesis, and reproduction, respectively, suggested itself. At the same time, the probable importance of wave-length of light in

connection with the above-named processes was fully realised. Shortly after the publication of the above conclusions (7), Shirley (31), working on the influence of light-intensity and light-quality upon the growth of flowering plants, reached the following results, which make an interesting comparison :—
(a) That a low intensity would suffice for the *survival* of the plants. (b) That a higher intensity was required for an increase in dry weight. (c) That flowering and fruiting were delayed by low intensities.

OUTLINE OF PRESENT INVESTIGATION.

The present investigation was undertaken with a two-fold aim, viz. :—

- (1) A further examination of these intensity limits and their accurate measurement.
- (2) An enquiry into how far the processes, phototaxy, photosynthesis, and reproduction must be regarded as wave-length phenomena.

Recent work dealing with the effect of light-intensity on plants goes to show that many plants have a narrow light-intensity range. In many unicellular water forms light is a determining factor in their distribution. Mobile forms seek out light of optimum intensity, and are repelled from regions of too high or too low intensity; Oltmanns (26), Englemann (9), and Wager (32) have stated this to be so in water forms of *Euglena*.

Euglena limosa is a mud form. It is present in its maximum numbers on the mud in summer, when it is exposed for many hours a day to bright sunlight. Therefore, we need consider only the lower intensity limits in relation to the life processes.

Apparatus for measuring light-intensity.

The use of the Watkins Bee Meter for measuring light-intensities in ecological work has been advocated by many writers, including Braid (7) in his general review of the various methods available to ecologists. I have found the instrument of the utmost value for a great deal of outdoor work, but decided to abandon its use in the present investigations for the following reasons. Firstly, the Bee Meter measures only the actinic rays, and, while for some biological processes we have every reason to believe that these rays are fundamentally important, there is the criticism that they are not the rays chiefly considered in the process of photosynthesis. It is, therefore, desirable to use a photometer, which is sensitive to a wider range of wave-length. Secondly, in the study of wave-length phenomena, it was necessary to use absorption filters. In some instances the filter employed cut out all or most of the rays which affect the actinometer, and so the instrument became useless.

Klugh (16, 17) has suggested several methods of light-measurement; Pearsall and Ulliyott (27) advocate a Bernheim photo-voltaic cell, and Atkins and Poole (1) have made prolonged studies of the use of the photo-electric cell with portable galvanometer for ecological work.

While I was engaged upon a study of these methods there came upon the market the "Weston Photronic Photo-electric Cell," which seemed to meet the requirements of the experiments.

The Weston cell is sensitive over a wide range of wave-length. The spectral response of the instrument as shown in fig. 1 is one which should be useful in biological work, having a range from 3000 Å. to 7500 Å., i.e. the visible and part of the ultra-violet radiation. With this instrument the correct illumination is read off in foot-candles by means of the pointer of a sensitive moving coil galvanometer. Measurements may be made from 1-500 foot-candles.

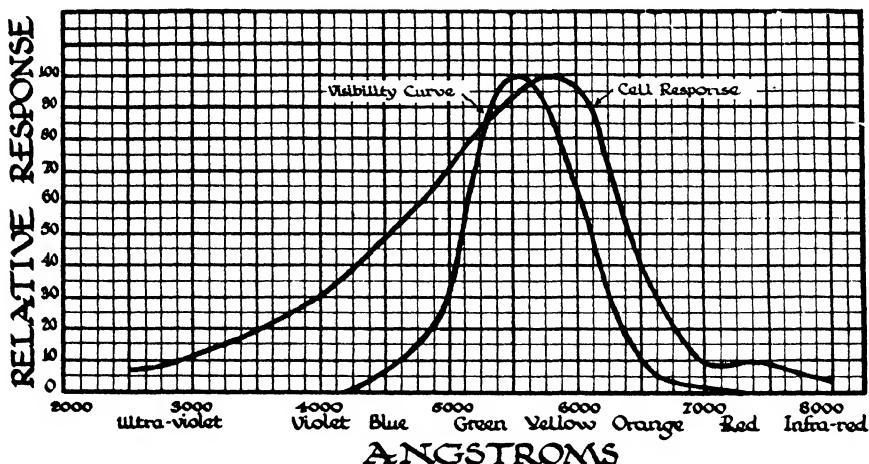


FIG. 1.—Spectral response curve of Weston Photronic Cell
with visibility curve of normal eye.

In using a photometer one must consider not only its spectral response and its maximum sensitivity, but also the direction of incident light and the quality of the source of illumination. In the Weston Cell the sensitive face is hinged. It can therefore be brought into the same plane as the surface of the mud on which readings are being taken.

Sources of illumination.

For the first series of experiments, and for the majority of the subsequent ones, daylight was used. Daylight, however, is not used in the calibration of the Weston Photronic cell (33).

In calibrating the cell, the makers employ a standard lamp of known colour-temperature (3000 °A.) and known candle-power. This is set up a known distance from the meter. A known number of foot-candles of light is therefore

shining on the meter. The position of the pointer on the meter is then marked with that number of foot-candles, and so the scale is fixed. By using daylight one is using the instrument to measure light, the quality of which is different from that used in the calibration. The colour-temperature of the light from the mid-day sun which reaches the earth's surface on a clear day is about 5400°A . In general the quality of daylight varies, but in these experiments it is safe to assume that it lies between the limits of colour-temperature 3000° A. and 5400° A. , and that it is permissible to use the scale marked on the meter uncorrected for all daylight illuminations. According to computations made

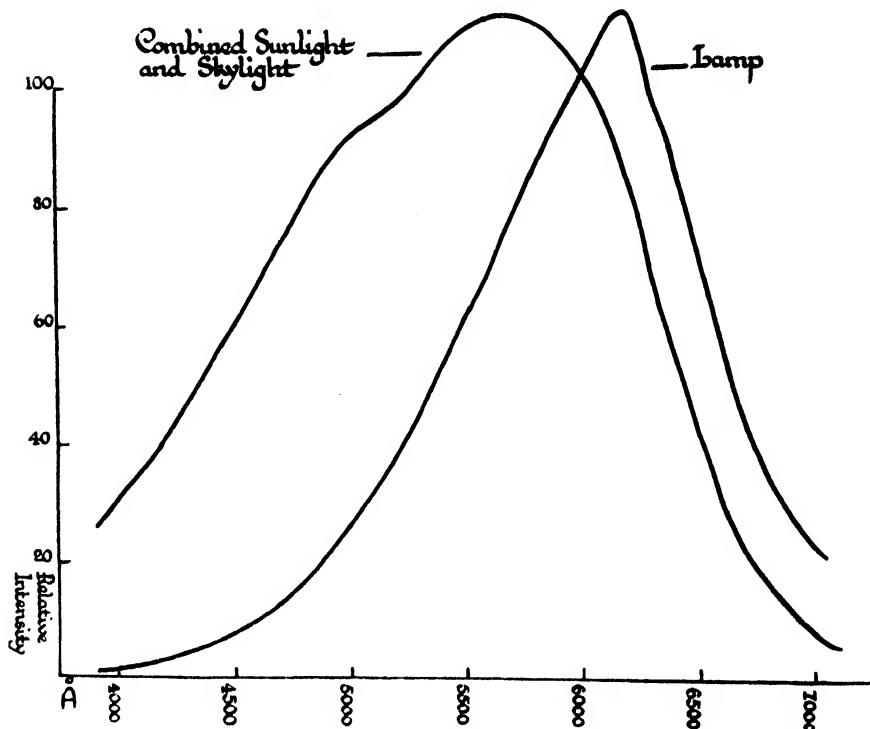


FIG. 2. (See below.)

the results will not be more than 5 per cent. out, and this is within the limits of experimental error.

For some of the experiments a 1000-watt lamp was used. Curves showing the quality of the light of the lamp as compared with daylight are given in fig. 2. The daylight curve is a combined sunlight and skylight curve.

Filters for dealing with light of different wave-length.

In recent literature there is much reference to the use of colour-filters for the examination of the effect of light of different wave-length on physiological

processes. Most of these deal with the rates of photosynthesis, growth, and reproduction, and will be dealt with in the sections on those subjects. Gard (11), working on *Euglena limosa* and using coloured glass of which he gives no spectral data, obtained contradictory results in his experiments. This may have been due to either insufficient regard for the interaction of factors or to lack of control of the quantity and quality of the light used. Working chiefly on phenomena of growth and reproduction Laurens and Hooker (19), Hurd (13), Stanbury (29), Klugh (15, 18), Meier (24, 25), Popp (28), Shirley (31), and Flint and McAlister (10) have used various forms of light filter, and have adopted somewhat different means of obtaining light of different wave-length, but of equal intensity. I decided, after studying these works, to try the use of Wratten filters and to measure the various intensities obtained by means of the Weston photo-electric cell. For this purpose computations had to be made (p. 28).

The six filters chosen, with data for transmission and wave-length, were :—

TABLE I.

No. of filter.	Total trans-mission.	Range of wave-length transmitted.	Range of wave-length with trans-mission greater than 10 per cent.
12	77	{ 5000-7000 Å. 3000-3300 Å. }	5000-7000 Å.
29	6·6	6000-7000 Å.	6100-7000 Å.
33	7·8	{ 3400-4800 Å. 6000-7000 Å. }	4400-4600 Å. 6100-7000 Å.
48	1·0	3200-5200 Å.	4300-5000 Å.
53	9·5	4750-6200 Å.	5200-5750 Å.
64	25	2600-6300 Å.	4000-5800 Å.

In fig. 4 (p. 39), a diagram shows the range and overlapping of the light transmitted by these filters.

It will be seen from these data that the filters vary considerably in density. If they had all been brought to the transmission of the densest (Klugh, 15), i.e. no. 48, with total transmission of 1 per cent., there would have been a danger of the light intensity falling below the minimum required to bring *E. limosa* to the mud surface.

It was decided to make measurements with the photometer at the time of experiment, and for this purpose several points had to be considered.

When a filter is placed over the cell, the current is reduced as the amount of energy transmitted is less. The amount of reduction will depend upon the absorption curve of the filter, the sensitivity curve of the photometer, and the

colour or spectral distribution of the source of light. It was decided to use good daylight as the source (p. 25). Experiments were performed at varying daylight intensities, but the majority at an intensity of 400 foot-candles.

A method was suggested whereby the readings obtained could all be compared on the same basis. The results may be expressed either in foot-candles or in relative energy units. The foot-candle is a unit of brightness, and suffers from the disadvantage that the eye is the basis of measurement, and consequently a foot-candle represents different quantities of energy in different parts of the spectrum owing to the variation of sensitivity of the eye with wave-length. On the other hand, the data available are not sufficient to express the results in absolute units of energy. Even in energy units, relative or absolute, the results must be used with caution when, as here, they sometimes represent the energy of a wide band of wave-lengths varying in intensity in an irregular manner.

For completeness, therefore, the values of light intensity on p. 37 (Table VIII) are calculated on both systems, taking control daylight as 400 foot-candles or 1000 energy units.

Briefly, the method is as follows :—The distribution of energy in the spectrum transmitted through a given filter is calculated from the data supplied with each Wratten filter. Graphs giving the response of the eye and the cell to this distribution are then constructed, and the ratio of the area bounded by these curves obtained, the scale chosen being one which gives equality of area when no filter is used. When the actual cell-readings are multiplied by these ratios the result is obtained in foot-candles, i.e. the brightness of the coloured light as it appears to the eye. To obtain the results in relative energy units the appropriate ratio by which the cell-readings must be multiplied is the ratio of the area of the energy distribution graph to the area bounded by a graph, the ordinates of which are the product of those of energy distribution and cell response.

General method of procedure.

Phototaxy.

Movement of *Euglena limosa* takes the form of burrowing periodically into the mud and re-appearing again upon the surface. Creeping over the surface of the mud in response to unilateral stimulation also occurs.

The appearance and disappearance of the organism in response to stimuli was watched by noting the shade of green colour on the mud.

The rate of response was also noted, and it was realised that factors other than light played an important part in determining both the nature and the rate of the response. Therefore, preliminary to the experiments on phototaxy a series of experiments concerning the effect and control of other factors was undertaken.

DETAILED DESCRIPTION OF EXPERIMENTS ON PHOTOTAXY.

The interaction of factors controlling the movements of *Euglena limosa* was soon found to be of a very complex nature. It was realised that an analysis of the effect of these factors would be pre-requisite to an understanding and correct interpretation of any movement observed. Owing to the seasonal periodicity and the necessity of repeating experiments under the same seasonal conditions, these preliminary experiments spread over several years.

Factors other than light which are known to affect both the nature and rate of response of *Euglena limosa* are :—

- (a) Number of organisms per unit area.
- (b) Temperature.
- (c) Water-content of mud.
- (d) Time of day.
- (e) Tide.

In addition, it is thought that there must be some inherent rhythm irrespective of these external stimuli. There is evidence that this is connected in some way with the age of the organism and its food-content. The inherent tendency of the organism to behave in a certain way is for the time being termed the factor "f".

(a) Number of organisms per unit area.

The Euglenae were counted by means of a shade-card in which each shade corresponds to the number present per unit area. The following values were selected :—

Shade I.	Approx.	5000	per square cm.
Shade II.	"	3800	" "
Shade III.	"	2800	" "
Shade IV.	"	1300	" "
Shade V.	"	500	" "

It was noticed that when the organisms were present in their maximum numbers (Shade I) they tended to react much more slowly than in cultures more thinly distributed.

(b) Temperature.

It was shown in a former paper (5) that *Euglena limosa* (then referred to as *E. deses*) moves most rapidly in response to stimuli at a temperature of 15° C., and becomes sluggish at temperatures below 5° C. or above 25° C.

(c) Water-content of mud.

It has also been observed (6) that *E. limosa* normally inhabits mud with a water-content of 88–99 per cent. (calculated on the air-dry weight). Further experiments have shown that in mud of this consistency *E. limosa* moves most rapidly. Soft and stiff mud were used in experiments (a) and (b) respectively,

and the water-content determined immediately after the experiment. Figures from a typical experiment are given below :—

TABLE II.

Date.	Temp.	Water-content.	Duration of tide.	Time of sunrise.	Time of experiment.	Behaviour of Euglena when placed in dark.
(a) 9. 5. 30.	16·4° C.	Per cent. 94	4–7 p.m.	5.0 a.m.	12.0 noon.	Disappear in 10 mins.
(b) "	"	56	"	"	"	Disappear in 35 mins.

Control experiments were set up and left in the light. In these cultures the mud remained green. Many similar experiments were performed, and the results in each case were consistent.

(d) *Time of day.*

It was observed that *E. limosa* will not burrow into the mud if placed in the dark a short time after coming to the surface. Accordingly a number of readings were taken to see how soon after their appearance they would respond to the stimulus and burrow. The results of two experiments are shown in Table III :—

TABLE III.

Date.	Water-content.	Temp.	Duration of tide.	Time of sunrise.	Time of experiment.	Behaviour of Euglenae when placed in dark.
22. 9. 31 . . .	Per cent. 90	15° C.— 16·5° C.	2–5 a.m.	6.42 a.m.	8 a.m. 10.0 a.m. 12.0 noon.	No change in 30 mins. Fade in 30 mins. Disappear in 15 mins.
10. 5. 34 . . .	93	15° C.— 16·5° C.	3–7 a.m.	5.15 a.m.	9.0 a.m. 11.0 a.m. 12.0 noon.	Slight fading in 30 mins. Disappear in 15 mins. Disappear in 10 mins.

Control experiments were kept in the light in which the cultures remained green.

Many similar experiments were carried out, and in all the organisms showed no, or very little, fading if placed in the dark less than two hours after their morning appearance.

Material examined at such time is usually in the 'mosaic' condition described by Gard (11) and myself (6). The Euglenae are rounded off, fitting closely into each other, and the eye-spot is generally hidden from view. A possible suggestion is that the movement up in the early morning has used up all the available energy. This suggestion is borne out by the fact that after a few hours, during which photosynthesis can take place, movement in response to a stimulus again occurs.

After several hours in daylight with plenty of manufactured food the organisms can be made to burrow, and re-appear repeatedly when placed alternately in light and in darkness.

(e) *Tide.*

Under natural conditions *E. limosa* burrows into the mud during periods of high tide. A tidal rhythm is visible for approximately three days, so that for this period the organism burrows at the time of high water even when removed from the river-bank. It is interesting to compare these results with those obtained by Bohn and Drzewina (4) with *Convoluta*, which may retain a tidal rhythm for a week.

That this tidal rhythm actually persists for longer than three days, though not visible without an additional stimulus, has now been shown. This is considered when dealing with the interaction of factors (p. 32).

(f) *Inherent behaviour of the organism.*

There are two points to be considered under this heading, and though they shed a little light on the problem of rhythm the real nature of the phenomenon remains obscure.

The first point is the occurrence of a burrowing when no apparent stimulation occurs, e.g. the tidal rhythm. On the river-bank the Euglenae are seen to fade just before the water reaches the spot. It would seem that the rhythm is induced by the tides of the days before. Other cases of burrowing without an apparent cause have been found to be due to the interaction of more than one external factor, and such movements are described under the next heading.

The second point is the question of individual variation, which seems to show very clearly in the rate of response. Subjected to a stimulus some cultures reach the shades IV. or V. very quickly, and remain like this for some time. Examined under the microscope, the slow-moving individuals appear a somewhat darker green. This colour has been found to be characteristic of the older individuals. Young cultures in the state of active division always move more rapidly than older ones, other conditions being the same. Thus

on the river-banks as the tide rises some old individuals are invariably left to be washed off the mud by the tidal waters.

The interaction of factors.

Under natural conditions, therefore, the organism is influenced by all these factors, external and internal. Some factors have a greater effect than others, e.g. the incoming tide will cause a burrowing when all other factors would permit of appearance on the surface.

In the course of experiment it was noticed, when a high-tide period came just before sunset, that the organisms made a much more rapid disappearance than when either of these factors was operating alone. The idea then came to me that possibly a response might be obtained by causing two factors to work together, neither of which was sufficient alone to produce a response. The two factors chosen were tidal influence and the effect of slightly reduced illumination. Normally a slight reduction in light intensity produces no response, neither does material removed from the river show tidal rhythm after three days. The material chosen for the experiment was removed from the river-bank in the morning on a day when high tide occurred from 2-4 p.m. Experiments were carried out at the time of high tide on the second, third, fourth, sixth, and eighth days after removal from the river. In each one, culture (A) was left in the light, and the other (B) placed at the time of high tide in a slightly shaded position. The results were as follows :—

TABLE IV.

Day after removal from tide.	Behaviour of Euglenae.	
	A.	B.
1. 2nd day	Disappear at time of high tide.	Disappear at time of high tide.
2. 3rd day	Gradual fading in half an hour at time of high tide.	Disappear in ten minutes at time of high tide.
3. 4th day	No change.	Disappear in ten minutes at time of high tide.
4. 6th day	No change.	Disappear in ten minutes at time of high tide.
5. 8th day	No change.	No change.

This experiment was repeated with similar results.

It will be seen that on the second day the Euglenae disappear at the time of high tide, as would be expected. On the third day the tidal rhythm was not so marked in A, although a gradual fading extending over half an hour could be seen. In B the organisms showed as rapid a disappearance as on the previous day. On the fourth day no tidal rhythm was visible in A, but the organisms in the shaded culture B again disappeared rapidly. On subsequent

days, when the tidal rhythm was completely lost, no change occurred in any culture, thus showing that the shading alone does not bring about the response.

Another possible instance of the interaction of factors is given under the conclusions to experiments on p. 40.

That some reactions are brought about by direct response to a stimulus, whilst others are the result of a rhythm is undoubtedly the case. There still seems some doubt whether the alternate burrowing and reappearing in accordance with alternating periods of day and night belong to the first or second category.

When kept in continuous illumination afforded by artificial light the organisms continue to burrow in the evening and reappear in the morning. That the evening burrowing may be due to deficiency in some region of the spectrum from the artificial source of light is likely, and is discussed on p. 36.

When kept in continuous darkness the organisms do not appear in the morning, and this, together with the observations in the previous paragraph, would seem to show that the upward movement is on the whole due to a direct stimulation rather than rhythm.

The control of other factors.

The foregoing observations on the effect and inter-relation of factors will suffice to show what care must be taken in order to prove that a result obtained is due to the factor under consideration, in this case light, and not to any other cause or combination of causes.

In all experiments, water-content and temperature were kept as near the optima as possible, and every attempt was made to cut out, or make allowance for, the effect of daily periodicity and tidal rhythm. Young active cultures respond more quickly, but these show the tidal rhythm; therefore discretion had to be used as to whether 'tidal' or 'non-tidal' material were better for the experiment in question. In the shorter experiments it was possible to use 'tidal' material in the morning when the tide occurred later in the day or vice-versa, though in the former case sufficiently long after sunrise (p. 30). The high-tide period on the river may last from fifteen minutes to three hours according to the position on the bank. Material was usually obtained from a position which is covered by the tide for two or three hours.

Shades II and III of the shade-card were used as starting-points in the experiments in order to cut out the possibility of over-crowding. Lastly, owing to individual variation in the rate of response, the *start* of the fading was noted in disappearance and the *first* tinge of green in reappearance. The time taken for complete fading or recovery was also noted.

Experiments on light intensities.

Daylight series.

In these experiments the source of light was diffuse daylight of 150–400 foot-candles depending upon the season. The place chosen for the experiments

was an unheated greenhouse with a north aspect. It was found that on a clear day the light intensity varied very little over two or three hours.

Group 1.

In the first group of experiments positions were selected in the greenhouse by the aid of the photometer, so that they covered a range of intensities. Cultures of *Euglenae* of the same shade (shade II) were placed in each position. A typical experiment is described below :—

TABLE V.

	Light intensity in foot-candles.	Behaviour of <i>Euglenae</i> .
1	70	No change.
2	60	" "
3	50	" "
4	40	Gradual fading in 60 minutes.
5	30	Disappear in 10 minutes.
6	20	" " "

When numbers 4, 5, and 6 were replaced in intensity 70 they recovered their original shade in about fifteen minutes. (This time varied somewhat during the course of experiment.) When replaced in intensity 50, a much slower and often only partial recovery took place.

Group 2.

A similar series of experiments was carried out, but this time the light intensity was cut down by using as filters a number of photographic plates which had been exposed varying amounts. By selecting from these it was possible to obtain the same range of intensities as those used in group 1.

Similar results were obtained, viz. the green colour tended to fade when the intensity fell below 40 foot-candles and to disappear when it fell below 30 foot-candles.

Group 3.

In this group of experiments cultures of *Euglena* were placed in the dark till all had disappeared. One culture was then placed in each of the light intensities mentioned above. It was found that the organisms fail to re-appear except occasionally in very small numbers at intensities below 50 foot-candles, while they rapidly regained their maximum appearance at intensities higher than this.

Artificial light series.

Using as source of light the lamps described on p. 26 an apparatus was fitted up so that *Euglenae* could be kept with a constant source of illumination,

A water-bath in which the water was constantly renewed was placed between the lamps and the cultures. Various intensities were obtained by placing the cultures at different distances from the lamps.

Group 1.

Cultures which were all similar in shade were placed at different distances, and the following results were obtained :—

TABLE VI.

	Intensity in foot-candles.	Behaviour of Euglenae.
Lamp	300	Fade in four hours.
	100	" " "
	60	Fade in $\frac{1}{2}$ hour.
	50	Disappear in $\frac{1}{2}$ hour.
	20	" " "
Control daylight	100 approx.	Remain at maximum until sunset.

Group 2.

In these experiments the cultures were kept in the dark until all the organisms had disappeared, and then one was placed under the lamp in each of the above intensities :—

TABLE VII.

	Intensity in foot-candles.	Behaviour of Euglenae.
Lamp	300	Reappear in maximum numbers.
	100	" " " "
	60	Reappear in small numbers (Shade V).
	50	No reappearance.
	20	" " "
Control daylight	100 approx.	Reappear in maximum numbers.

These experiments were repeated with the addition of a mercury vapour lamp in order to supply ultra-violet radiation. No difference was observed in the results.

Conclusions.

From the above experiments the following conclusions may be drawn :—

- (1) The illumination measured with photometer at which *E. limosa* burrows into the mud appears to be between 30 and 40 foot-candles of daylight.
- (2) A somewhat higher intensity, viz. 50–60 foot-candles, is required to bring the organisms to the surface. The considerable difference is probably due to

the fact that some of the total light intensity is cut down by the surface-particles of mud under which the organisms are lying.

(3) Under the lamp the intensity at which the organisms burrow, *measured with the photo-electric cell*, is much higher than that at which they burrow in daylight. An examination of the lamp-curve given in fig. 2 shows that the maximum energy from the lamps is at 6100 Å., while for daylight (combined sunlight and skylight curve) it is at 5700 Å. (see pp. 25, 26). The spectral response curve for the cell is highest at 5720 Å., and therefore a great deal of the energy producing the high reading is derived from this region. Apart from this, if we again compare the daylight and lamplight curves we see that there is a large area under the daylight curve between the wave-lengths 4000 Å. and 5800 Å., which is absent from the lamp-curve, i.e. the lamp as compared with daylight is deficient in rays at the blue end of the spectrum, which we have reason to believe are of greatest importance in promoting phototactic movement. In the earlier readings (6), taken with the Bee Meter sensitive chiefly to the blue rays, there was always a very constant correlation between the readings and the intensity at which *Euglena* disappeared and reappeared.

In using the cell, however, there was no such striking constancy, especially at times of bright red sunrise or sunset, when the quality of the daylight would be outside the limits allowed for in the 5 per cent. correctness given on p. 26.

In the next series of experiments, therefore, attention is devoted to the importance of wave-length in the phenomenon of phototaxy.

EXPERIMENTS ON WAVE-LENGTH OF LIGHT.

In the study of the effect of light of different wave-length on the movements of *E. limosa* four types of experiment were undertaken. The difficulties of controlling other factors were considerable, and five years of experiments were carried out at different stages of the day, the tide, and the season in an attempt to eliminate as far as possible the effect of such factors.

In each experiment the mud of uniform water-content and covered with a uniform shade of green was spread out in flat dishes. The filters mounted in glass were lodged in small zinc cylinders 2½ inches deep and 3 inches in diameter (fig. 3 a). The filters rested on small ledges on the inside of the cylinder. The whole cylinder was sunk about an inch into the mud. The filters merely rested on the ledge and so air could circulate. During darkness they were removed into order to avoid any oxygen deficiency.

The experiments performed may be grouped into four types :—

1. *Material in which no other factor causing burrowing was operating.*

These experiments were carried out on material which had been long removed from tidal influence, in the middle of the day and in the summer. The light-intensity in the greenhouse during these experiments was 400 foot-candles,

and in any one experiment only varied a very small amount. (If the light-conditions varied unexpectedly owing to storm-clouds etc., the experiment was abandoned.) In the Table given below light-readings in foot-candles and in relative energy units are given as described on p. 28.

Under such conditions of experiment the results obtained were as follows :—

TABLE VIII.

No. of filter.	Total range of wavelength.	Range of wavelength over 10 per cent. transmission.	Intensity in foot-candles.	Intensity in relative energy units	Behaviour of Euglena.
12	5000-7000 Å.	5000-7000 Å.	293·4	530	Slight fading.
29	6000-7000 Å.	6100-7000 Å.	30·5	257	Disappear in 30 minutes.
33	{ 6000-7000 Å. 3400-4800 Å.	{ 6100-7000 Å. 4400-4600 Å.	35·7	{ 254 16 }	No fading.
48	3200-5200 Å.	4300-5000 Å.	6·4	54	No fading.
53	4750-6200 Å.	5200-5750 Å.	35·1	31	Disappear in 1 hour.
64	{ 2600-6300 Å. Daylight. Darkness.	{ 4000-5800 Å.	106·6 400	194 1000	No fading. No fading. Disappear in 30 minutes.

2. Material in which some other factor causing burrowing was operating.

These experiments were carried out on material in which some stimulus other than light was expected to operate. Two stimuli were studied : (a) approaching darkness, (b) approaching high tide. In each experiment the filters were put on at the onset of the action of the stimulus. In them increased shading hastened the process.

The results in all experiments was the same.

Those under filters 29 and 53 disappeared first, those under 12 next, and those under 33, 48, and 64 last. The control was always much greener than the cultures under the filters at the end of the experiment.

3. Material which had been covered by filters before sunrise.

In this series of experiments the filters were placed over the cultures just before sunrise. The cultures were examined when the control had become green.

The results showed that the cultures under filters 48, 33, and 64 were greenest, under 12 pale green, while under 29 and 53 no green colour was visible. Later in the day, however, those under 53 had become green.

4. Material which was illuminated from one side only.

In these experiments a piece of black paper was pasted over the filter so as to allow light to enter only from a sector at one side (fig. 3 *b*).

Examined after two hours the organisms had moved towards the light under nos. 33, 48, and 64. Later, after six or more hours they had moved towards the light under filter 53. Left for several days they could be seen crowding towards the light in these four, but no instance of moving towards the light was seen under filters 12 or 29.

From these experiments it will be seen that under filters 33, 48, and 64 the behaviour of the organism approximates to that in daylight and under filter 29 it behaves as in darkness. The results under filters 12 and 53 are variable, and will be discussed below.

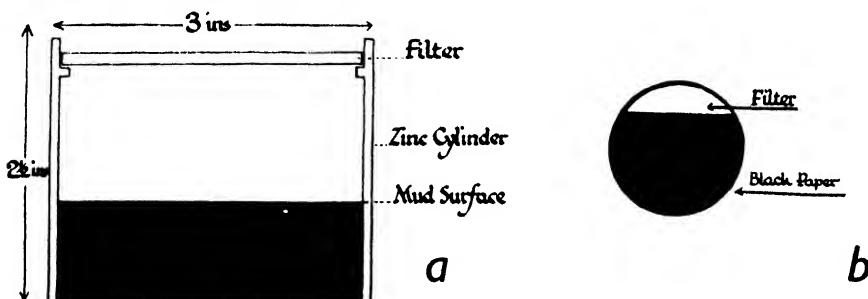


FIG. 3.—Apparatus used for filter experiments :—*a*, section of zinc cylinder with filter in position; *b*, filter covered with black paper except at one side.

Conclusions.

Taking each filter in turn we can study the results obtained and draw conclusions from them :—

1. Filter 64. (Blue-green.)

This filter has a wide range of wave-length, 2600–6300 Å., and an intensity of 106 foot-candles, or 194 energy units under the conditions of the experiment. As would be expected, Euglenæ under this filter behave as in daylight.

2. Filters 33 and 29. (Red.)

The most instructive results in the investigation were obtained from a comparison of the behaviour under these two red filters. It was pointed out earlier (p. 28) that quantitative estimates of energy must be used with caution when dealing with filters of varying opacity and range. Between filters 29 and 33, however, a safe comparison may be made because in the two, the distribution of transparency between Å. 6000 and Å. 7000 is very similar. The energies of the 6000–7000 band are nearly equal for the two filters, being

270 for filter 33, and 257 for filter 29; but filter 33 also transmits a weak band between \AA . 3400 and \AA . 4800, and a large proportion of this addition is in the range \AA . 4400-4600.

We may assume, therefore, that this is the effective band in causing response to the light-stimulus, i.e. the organisms remain on the surface of the mud.

3. Filter 48. (Blue.)

The results obtained with this filter must be considered with those obtained for filter 33. With filter 48 we have a low intensity 6.5 foot-candles or 54

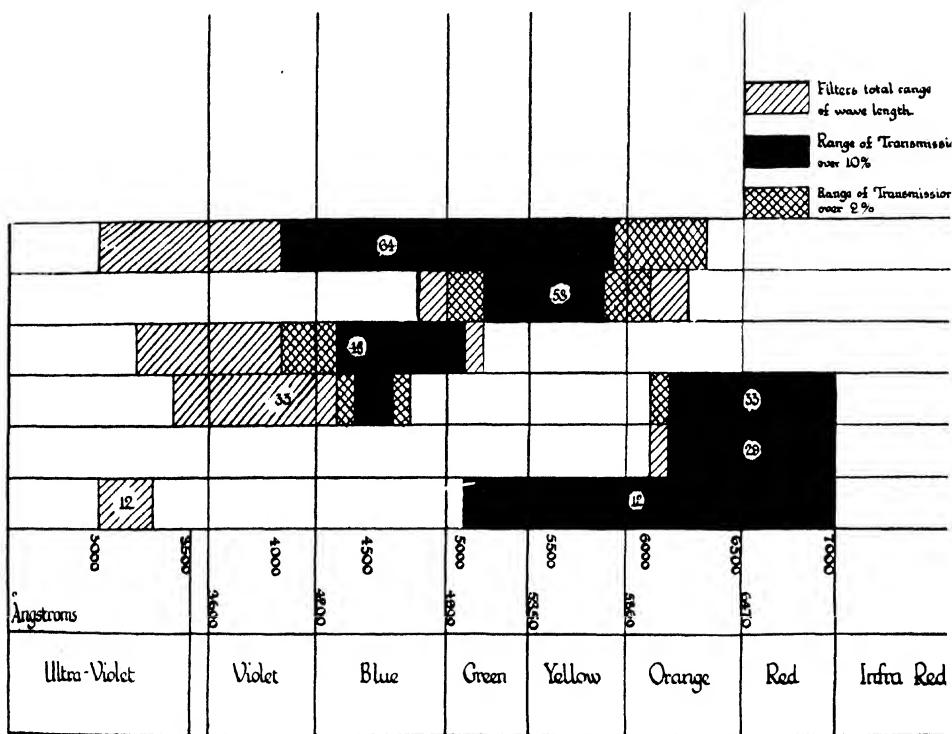


FIG. 4.—Diagram to show range of wave-lengths transmitted by Wratten Filters 12, 29, 33, 48, 53, and 64.

energy units, of which 70 per cent. lies within the region \AA . 4400-4900, yet the Euglenae remain on the mud surface under this filter. Again, we have evidence of the efficiency of this region of the spectrum in producing a response to the light-stimulus.

4. Filter 12. (Yellow.)

With this filter we have a much higher intensity, viz. 294 foot-candles or 530 energy units. It has a transmission of over 10 per cent. in the band

\AA . 5000– \AA . 7000. Here, therefore, ten times the amount of energy transmitted by the band \AA . 4400–5000 in filter 48, but spread over the range \AA . 5000–7000 does not prevent fading. It has been shown that under filter 12 the Euglenae come up in the morning with a feeble response, but when illuminated from one side no response is seen. Under filter 29 there is no such response.

Filter 12 has a strong band between \AA . 5000 and \AA . 6000, which Filter 29 has not. We have seen that there are other factors which may cause the moving of the organism *up and down* which do not affect a sideways movement, and one which is important here is the diurnal rhythm. Organisms kept in the dark do not appear in the morning, nor when kept under filter 29. It may be, therefore, that radiation between \AA . 5000 and \AA . 6000 *plus a diurnal rhythm* may produce a response, though neither will do so when working alone.

5. Filter 53. (Green.)

In this filter we see that there is very low intensity, 35.1 foot-candles or 31 energy units. It has a range of wave-length similar to no. 12, but in addition extends into the blue, with a transmission of less than 2 per cent. as far as \AA . 4600. With this filter the organisms usually behave as in darkness, though the intensity under this filter is not much less than under 48. As this filter *does* in time produce a response to one-sided illumination and no. 12 does not, we must conclude that the rays in the very weak band \AA . 4600–4900 transmitted by no. 53 do produce a response, given a long enough duration of action.

Mast (23) has given a full list of results obtained by workers on the relation between spectral colour and stimulation in the lower organisms. It is difficult to compare the present results with these and many subsequent ones, since the methods employed for the measurement of light, of different wave-length but equal energy, do not permit of direct comparison.

One may, however, mention two results where apparatus similar to that used here was employed in the investigation of related phenomena :—

1. Laurens and Hooker (19 and 20) investigated the sensibility of *Volvox* to radiation of different wave-lengths, but of the same intensity. They used two criteria, viz. duration of presentation time and rate of locomotion. By both methods they found a narrow band around \AA . 4940 to have the maximum stimulating value, decreasing up and down.

2. Johnston (14) found maxima for phototropic curvatures in etiolated *Avena* coleoptiles in the two regions \AA . 4400 and \AA . 4800.

SUMMARY.

1. Several factors control the movements of *E. limosa* up and down in the mud. The interaction of these factors is of a complex nature, and it is often difficult to ascribe a given response to the action of any one factor. It has here been definitely established that a slight stimulation by two factors, each of which is insufficient alone to bring about a response, will do so if operating together. This has been demonstrated repeatedly in one case, namely, the

simultaneous action of very slight shading and weak tidal rhythm, and appears to be the probable explanation in another case, viz. diurnal rhythm and radiation *near*, but not *in*, the wave-length band of maximum efficiency.

2. In daylight a minimum light-intensity of 33–40 foot-candles is required to *Maintain* the organisms upon the surface of the mud, while a minimum of 50–60 foot-candles is required to *bring* them to the surface.

3. Using artificial light, viz. 1000-watt lamps, the intensities at which the organisms burrow is much higher, but the high readings are derived from strong radiation in the red end of the spectrum, the artificial light being deficient in the band Å. 4000–5800.

4. The importance of light quality was therefore considered. Wratten filters were used and computations were made whereby the intensities of light transmitted by these filters could be compared both in foot-candles and in relative energy units.

5. Radiation in the band Å. 4200–4600 is the most effective in producing a response. That wave-length is more important than total energy is shown best by a comparison of two red filters (Wratten filters nos. 29 and 33), in which the distribution of transparency and the energy is nearly equal. The one (no. 33) under which a response occurs has a weak band in the region Å. 4200–4600, while the other (no. 29) under which no response occurs has not. Results obtained by the use of other filters support these conclusions.

I should like to express my sincere thanks to Professor A. M. Tyndall and Mr. M. G. Bennett for the computations given on p. 28, and for much help and advice; to Mr. S. E. Williams for the curves given in fig. 2; to Professor Skene for reading the manuscript; to the Colston Research Society for a grant towards the purchase of apparatus; to the Weston Instrument Corporation Ltd., and to Eastman Kodak Ltd. for permission to reproduce data given in their publications.

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Studies in the Capparidaceae.—I. The life-history of *Cleome Chelidonii* Linn. fil.

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(PLATE 8 and 54 Text-figures)

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HISTORICAL INTRODUCTION.

THE family, under the name Capparides, was first created by Bernard de Jussieu (1789) in a list deposited in Louis XV. Botanical Gardens in 1759. In this were included nine genera which comprised not only some true Capparidaceous types like *Cleome*, *Capparis*, and *Crataeva*, but also others of what are now regarded as kindred families like *Viola*, *Reseda*, *Tropaeolum*, etc. Subsequent workers added to and removed from the family various other genera, and the general tendency was to increase the prevailing disorder of the group. For example, Adanson (1763) removed *Viola*, but put in *Vitis* and *Passiflora*. De Candolle (1824) banished some of these extraneous genera, but put in others, and the number was swollen to seventeen. Endlicher (1841) still further increased the number to twenty-four, and these he brought under two tribes, the Cleomeae and the Cappareae. *Roydsia* was brought under *Capparideis affine* separately. Lindley (1853) distinguished twenty-eight genera with 340 species. Baillon (1872) admitted seventeen genera with 300 species, while Bentham and Hooker (1862) listed twenty-three 'conspectus' genera together with ten formae abnormes. Engler and Prantl (1891) recognised thirty-four genera. Of these, the number of Indian genera as reported by Hooker (1875) is eight.

The Capparidaceae have been divided into two tribes, the Cleomeae and the Cappareae, the former with dry capsular fruits dehiscent by their walls and the latter with fleshy fruits. Though Baillon (1872) put *Maerua* in a separate tribe, Engler and Prantl (1891) conform to the original division of the family into the Cleomoideae and the Capparidioideae, with a third tribe Dipterogioideae.

The affinities of the Capparidaceae have been recognised by the earliest workers. Its close resemblance to the Cruciferae was responsible for some of the Cruciferous genera being included by some of the earlier workers. Lindley (1853) assigns to it a position between the Passifloraceae and Flacourtiaceae, flanked by Brassicaceae and Resedaceae. Eichler (1878) says 'die Verwandtschaft dieser Familie mit den Cruciferen ist so innig, dass manche Formen, namentlich aus der Gruppe der Cleomeae, sich kaum durch das nicht entschieden tetrodynamische Androeceum von Kreuzblütlern unterscheiden lassen'. Baillon (1872), emphasizing its close relationship to 'the Papaveraceae and the Cruciferae, says that of the first it lacks the double corolla, copious

albumen, and milky juice. Through *Cleome*, especially the types with a dry siliquiform dicarpellary fruit and a hexandrous androecium, we are brought so near the Cruciferae that the only absolute distinction lies in the habit and the false septum in the fruit of the latter.

The Capparidaceae are chiefly tropical. *Steriphoma*, *Atamisquea*, and *Wis-lizenia* are tropical American (Baillon, 1872), while *Apophyllum* and *Emblingia* are Australian. Four genera—*Thylachium*, *Euadenia*, *Boscia* and *Ritchiea*—are tropical African. *Capparis* and *Cleome* are widely distributed throughout the tropics, and one species, *Polanisia graveolens*, has been recorded as far north as Canada (Lindley, 1853). *Capparis spinosa*, the common Caper, is a native of the most southern part of Europe. Economically the family is not of any great importance. The European capers are well known for the use made of their flower-buds as a stimulant aperient digestive condiment. Some of the older writers have mentioned medicinal properties. Lindley (1838) says that the acrid root of *Capparis cynophallophora* is specific for dropsy, while the bark of *Crataeva Tapia* is used as a cure for intermittent fevers. The leaves of *Crataeva religiosa* are prescribed as a stomachic (Oliver, 1868).

Cleome is a Linnaean genus (Linnaeus, 1735). It is placed under Tetradynamia subgroup Fructu Siliquosa along with *Brassica* and *Raphanus*. A reference to the *Index Kewensis* (1893) shows that *Cleome* has had to that date thirty-five synonyms, one of the chief being *Polanisia*.

Cleome Chelidonii was first described by Linnaeus fil. (1781) under the group Tetradynamia Siliquosa. It is interesting to note that the original plant on which Linné based his naming was collected by Koenig in Tanschaur (Tanjore in south India). In describing the corolla of the plant in question, Linné says that it is 'rubra, figura Chelidonii hybridri'. Hence it is clear that the specific epithet is after the Papaveraceous genus *Chelidonium*. Bojer (1843) described a species of *Cleome* as *Polanisia strigosa* (? *C. Chelidonii*), but it differs from the Linnaean species in the definiteness of the number of stamens. Oliver (1868) separated *strigosa* of Bojer from *Chelidonii*, and since then the Linnaean species has been kept in use, while the species of Bojer is retained as *strigosa*. *Cleome Chelidonii* has been described under the name of *Polanisia* by De Candolle (1824), and its occurrence has been indicated to be India. It abounds in the east coast of south India, and as reported by Roxburgh (1832), it delights in rice lands, and appears immediately after the first rains.

Very little morphological work appears to have been done on the Capparidaceae. The paper of Hilaire and Moquin Tandon (1830) is the earliest that I have found which deals in a meagre way with some morphological aspects of floral symmetry and the insertion of the floral whorls on the receptacle. Payer (1857) gives a few details of the sequence of appearance of the floral whorls of *Cleome*, *Capparis* and *Polanisia*. Brandza (1891) includes the Capparidaceae also in his general account of the development of the integuments of the ovule in several families. Guignard (1893) gives a short note on the histology of the integuments of *Polanisia graveolens*. Eichler (1865) gives few details of the

floral organogeny of a few Capparidaceous types. Orr (1921 b) has made a few observations on the structure of the integuments of *Cleome* and *Isomeris*. He has also recorded the occurrence of nucellar tracheids in *Steriphoma cleomoides* (Orr, 1921 a).

The only recent paper that I have seen is that of Mauritzon (1935) dealing with the embryology of a few types of Capparidaceae. Rao (1936) gives a short account of the embryo-sac formation in *Maerua*. Hedayetullah (1935) publishes a short note on the embryo-sac formation in *Capparis horrida*. The Capparidaceae have, however, come in for some casual mention at the hands of a few anatomical workers. This has been occasioned by the controversy on the morphology of the Crucifer carpels and those of the Papaveraceae, and some have made casual mention of the closely allied Capparidaceae in that connection. Among these mention must be made of Saunders (1923), Eames (1931), and Eames and Wilson (1928). In this, the first of a series of papers, I propose to deal with the life-history of *Cleome Chelidonii*, and, having this as the type, a comparative study of some of the other genera on which I am working will be made. The present paper will be confined to a statement of observed facts in respect of the developmental morphology of *Cleome Chelidonii*, and any discussion on the morphology of the carpel with which is associated the theory of carpel polymorphism will be reserved for a future paper.

MATERIALS AND METHODS.

Materials for the present investigation were collected at Annamalainagar in south India, where the plant occurs in profusion on the borders of paddy-fields soon after the rains. I wish to express my indebtedness to Mr. K. R. Venkatasubban, M.Sc., for making available further material found to be necessary while work was in progress. The investigation was carried out in the Botanical laboratories of the University of London, King's College, under the guidance of Professor Ruggles Gates, F.R.S., whose valuable help and criticism I wish gratefully to acknowledge. Collections were made between 10 a.m. and 4 p.m. on bright sunny days, and fixed on the spot. A variety of fixatives was used, comprising Navashin's fluid (McClung, 1929), chrom-acetic-formalin of Karpetschenko and Langlet (Manton, 1932), B 15 (McClung, 1929), corrosive sublimate-formalin-acetic-alcohol (Chamberlain, 1932). With most of these a prefixation in Carnoy was found desirable, especially in the fixation of young flower-buds. An exhaust-pump was invariably used to aid proper fixation. For older stages, like mature ovaries and ovules, formalin-acetic-alcohol (Chamberlain, 1932) and Weinstein's modification of Licent's fluid (Weinstein, 1926) were found to be most suitable. The sectioning of the mature seeds gave immense difficulty on account of the hard testa. Prolonged immersion varying from one to three days in strong and 80 per cent. glacial acetic acid was tried with some success, though perfectly whole sections of the entire seed could be got only rarely, the bulk of the cotyledons flying off as soon as they were cut,

THE ONTOGENY OF THE FLOWER.

The first sign of the flower is a knob-like protuberance in the axil of a leaf. The organs of the flower arise in acropetal succession. After the petals have been initiated, the terminal axis broadens a little below the apex, on whose surface the primordia of the stamens arise as small club-shaped projections (Pl. 3, fig. 1, *s*). These arise by periclinal divisions of the cells of the hypodermal layer of the broadened disc which surrounds the centrally situated rounded apex (Pl. 3, fig. 1, *a*). It is from this central domed apex that the primordia of the carpels are initiated. A careful examination of this region reveals that the primordia originate on the sides of the apical dome, and not terminally (Pl. 3, fig. 2, *l*). A photomicrograph of this region at a later stage (Pl. 3, figs. 3 & 4) shows that there are three distinct deeply staining tissues, of which the two lateral ones represent the carpel-initiating cells, while the central portion undoubtedly represents the terminus of the apical dome, whose cells still being meristematic prior to eventual inactivity are characterized by dense cytoplasm. This seems to indicate clearly that the carpels are definitely lateral in origin, and not terminal. Newman (1936) has recently proved the lateral origin of the single carpel of *Acacia suaveolens*.

Each carpel arises as a papilla, and, as the two roll in, their edges almost meet, so that in very young ovaries two small loculi are seen on either side of the broadened commissural region. As the gynoecium gets older the two loculi increase in size, the commissures gradually separate, and eventually a single ovarian cavity is formed (Pl. 3, fig. 5). About the time the carpels appear, the sepals show the growth of epidermal glandular hairs (fig. A 1), which are confined to the dorsal surface. The two whorls of sepals seem to originate almost simultaneously, though there is a slight indication of the median pair preceding the lateral. Rendle (1925), discussing the absence of bracteoles in the Cruciferae, says that the evidence of their existence at some time in the history of the family is found in the position of the outer whorl of sepals, which are median, and not lateral, as we should expect them to be in the absence of bracteoles. Arber (1931), on the contrary, proves by a study of the ontogeny of the floral organs that, though the median pair of sepals are outer, the lateral pair are really the lower (first to make their appearance), and at a very early stage are enveloped by the median ; this, she considers, is in keeping with the absence of bracteoles. The Capparidaceae, like the Cruciferae, do not have bracteoles (Rendle, 1925), and the arguments that apply to the Cruciferae apply as well to this family. From a study of the ontogeny of the floral whorls based on serial sections there seems to be no evidence for considering the median sepals as the inner.

THE OVARY.

The ovules are arranged in four rows on the parietal placentae of the bi-carpellary ovary (Pl. 3, fig. 5). The pairs on either side of the centrally projecting commissure are not, however, on the same level. Further, the ovules

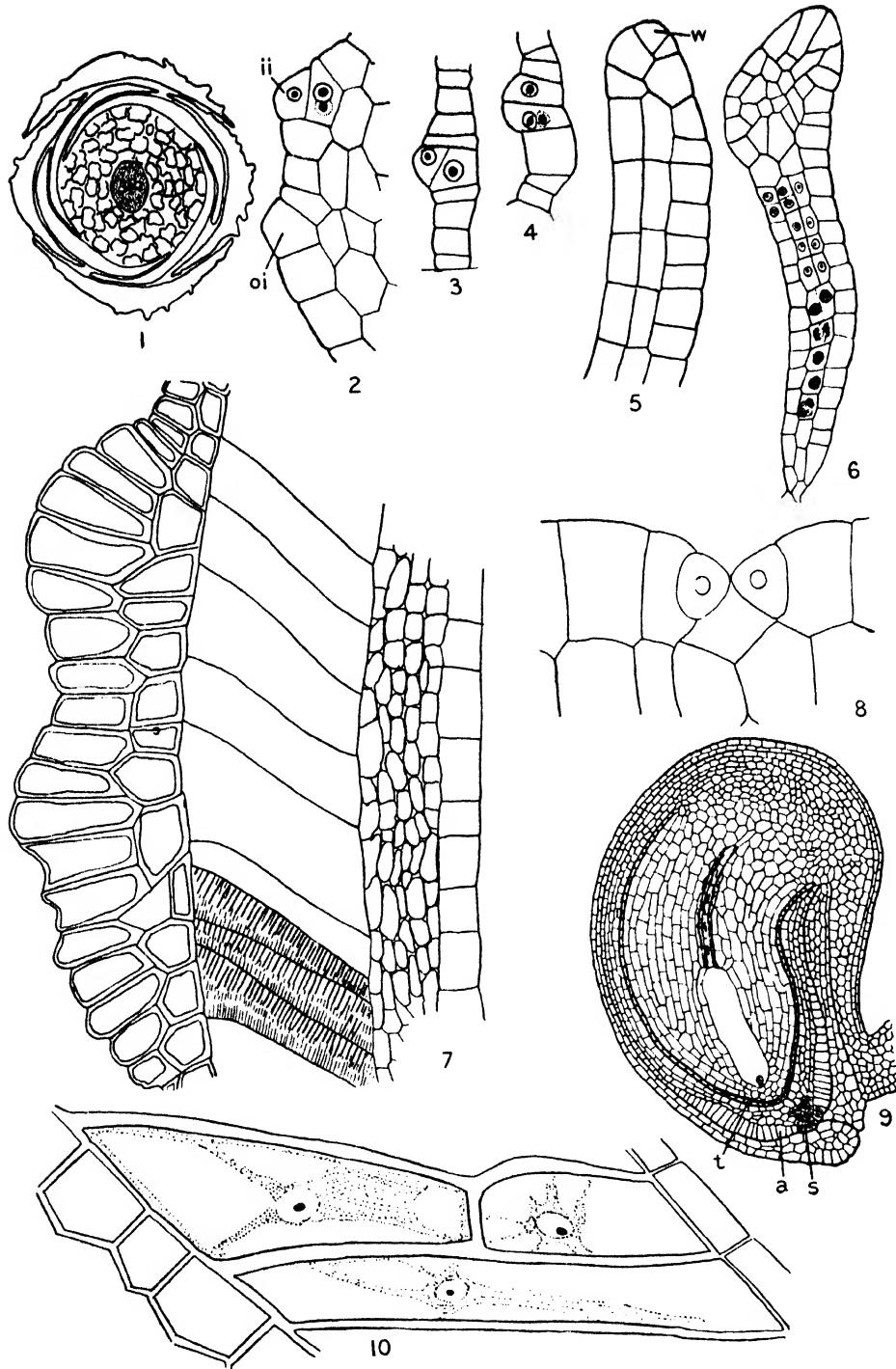


FIG. A. (For Explanation of Text-figs. A-E see pp. 70-72.)

in each pair are equally spaced, and are really alternating, so that the maximum number of ovules are packed in the available space. The two placentae are situated on either side of a central hemispherical knob, the commissure. From the placentae arise the ovules, which in the primordial condition resemble four rounded projections, prominent on account of their cells being more compact, and having denser cytoplasm. The vascular tissues of the ovary-wall at this stage of development of the ovules consist of only procambial strands, and their arrangement gives an indication of the general pattern of their future disposition. It is remarkable that there is no well-marked mid-rib in either of the valves, and the biggest of the carpillary strands are the commissural, of which frequently two occur close to one another at the region of contact of the two carpels (Pl. 3, fig. 5, *r*). The double nature of these commissural strands could sometimes be recognised, even at a much later stage (Pl. 3, fig. 6), when the bundles have become definitely organized, and vessels have made their appearance, and in some a definite depression could be seen between these two bundles. There are about six procambial strands in each of the two valves at the time of differentiation of the ovules, but soon after fertilization the number increases to about eighteen. It is only at about this time or slightly earlier that the placental strands, inverted in their orientation with reference to the commissural bundles, are evident, though the procambial strands of these are seen even in very early stages (Pl. 3, fig. 5, *p*).

Stomata are present in the outer wall (abaxial) of the ovary. These have the same structure as the stomata in the leaves of the plant (fig. A 8). Orr (1921 *b*) has noted stomata in the inner ovarian wall of *Cleome spinosa* and *Isomeris arborea*. None were found, however, in the inner wall of the ovary of *Cleome Chelidonii*.

THE INTEGUMENTS.

About the time the primary parietal cell is being cut off from the archesporial initial of the ovule, the primordia of the integuments arise as annular out-growths at the base of the nucellus (Pl. 3, fig. 7). The inner integument appears slightly earlier than the outer, and its origin is superficial, only the epidermal cells of the nucellus taking part in its formation (fig. A 2, *ii*.). One of the cells of the epidermis at this region becomes conspicuously big, and divides by the formation of oblique walls (fig. A 3), as a result of which a triangular wedge-shaped cell is cut off, while simultaneously the adjoining epidermal cells divide radially, by which an increase in the cell-mass is brought about. Sometimes radial division of the superficial initial precedes the oblique wall-formation (fig. A 4). Subsequently, the cells enveloping the wedge-shaped cell divide repeatedly by transverse walls, culminating in the production of an integument of two layers of cells. Though the outer integument is initiated slightly later than the inner, its growth is very rapid, especially the outer half, which nearly covers the top of the nucellus, overtaking the inner integument by the time barely about five layers of wall-cells have been organized (Pl. 3,

figs. 8 & 9). By the time the tetrad is formed the two halves of the outer integument come together and form a micropyle, while the inner integumental halves are yet widely apart. Discrepancy in the rate of growth of the two integuments seems to be a feature of common occurrence in Angiosperms. Mauritzon (1935) has observed this in all the Capparidaceous genera that he investigated, while Cooper (1931, 1933) has found it in *Melilotus* and *Lycopersicum*. The halves of the inner integument in *Cleome* come together a little later, when the embryo-sac is in its binucleate condition, and the full micropyle that is thus formed presents more or less a zigzag appearance (Pl. 3, fig. 10).

Initially the two integuments, except the ventral half of the outer, consist only of two layers of cells ; each integument has a triangular wedge-shaped cell at the tip (fig. B 23, w). But when the outer integumental halves close together, its micropylar region becomes more massive, consisting of four to five layers of cells (Pl. 3, fig. 9). This is the result of the repeated and somewhat irregular division of the wedge-shaped apical cell. The inner integument follows the same procedure, but it ultimately becomes much more massive than the outer, becoming several cells in thickness throughout. Unlike the outer integument, which remains two-layered right from its inception till a late stage in the development of the seed, the inner becomes three-layered by the time that the tetrad is organized, and this is attained by the simultaneous tangential division of the cells of the inner layer (fig. A 6) and at the four-nucleate stage of the embryo-sac there are four layers constituting the inner integument. The micropylar region is, of course, very massive. In this region there occur at about the time of fertilization, conspicuous patches of thick-walled elements, characterized by reticulate thickenings (fig. A 9, s; fig. E 54, s). In the meantime the outermost layer of the inner integument, especially the cells bounding the micropyle, shows marked radial elongation.

The appearance of the ovule at this stage is so very similar to that of *Gnetum* that one is tempted to draw a comparison. In *Gnetum Gneemon* (Pearson, 1929) the outer envelope is thick and succulent, forming the outer coat of the seed. The middle envelope is thinner, of which the fibrous elements form the stony layer of the seed-coat. This increases in thickness where it surrounds the micropyle. At this region the layer outside of the stony layer consists of radially elongated cells, very closely similar to those found in *Cleome*, and this Pearson calls the expanded soft outer layer. Leaving out of consideration the innermost of the three envelopes, which is concrecent below with the nucellus, one is almost tempted to say that the two are homologous ; for not only is there similarity in the radially elongated cells of the inner of the two integuments in both, but the stony layer constituting the inner layer of the inner integument in *Gnetum* bears resemblance to the corresponding layer in *Cleome*, where it becomes early differentiated from the rest of the layers by the cells becoming bigger and their walls sclerotic (fig. A 9, t). This sclerotic layer forms an essential part of the future seed-coat. These radially elongated

cells, which originate as a micropylar cap, gradually extend all round the nucellus as the seed gets older, and the sclerenchyma patches also extend right over the nucellar apex and merge into this layer (text-fig. E 54 *a*, *s*, & Pl. 3, fig. 12). The walls of the cells of this layer become lignified, and they show pitted and scalariform stratifications (fig. A 7). The cells become many times as broad as they are long, and they retain their nuclei till a very late stage (fig. A 10). They are largely vacuolated, and on this account Orr (1921 *b*) calls this layer the aqueous tissue. In the mature seed these cells are seen to contain crystals, presumably of silica. There can be little doubt that the fibrous layer thus formed in the seed functions as a protecting envelope, preventing dessication of the embryo. But Orr (1921 *b*) believes that its genesis in the organic apex of the inner integument, its interrupted development, and the retention of the living contents all seem to suggest another function at the time of its inception.

Guignard (1893) found the external integument of *Polanisia graveolens* to consist of two layers and the internal of five to six layers, of which the outermost is said to become sclerotic. Nothing is said of their form. Mauritzon's (1935) account is not detailed on this point. According to him, there is some difference between the *Cleome* and the *Capparis* types. In the former it is essentially the same as described above, though no mention is made of the stratifications on the walls of the aqueous tissue cells or of the sclerotic innermost layer of the inner integument. However, in *Tovaria pendula* he observed net-like striations on the walls of the cells. In the *Capparis* type, on the other hand, not only are there more layers of cells constituting the inner integument, but the outer layer is undifferentiated from the rest. Radially elongated cells, Malpighian cells, have been found in Leguminous seeds and in many other plants. But these, according to Pammel (1899), constitute the epidermis of the testa and do not belong to the inner integument.

As the ovule matures into the seed the cells of the outer integument, especially the outer layer, elongate radially at definite intervals, so that short spinous projections ultimately result (text-fig. A 7, E 54, and Pl. 3, fig. 13). These two layers become heavily suberised and lose their individuality. The already radially elongated cells of the aqueous tissue elongate still further, and their walls become greatly lignified, the stratifications being of the pitted and the scalariform type. The innermost layer of the inner integument, which was early distinguished from the others by becoming bigger and undergoing lignification, forms a definite envelope surrounding the embryo (Pl. 3, fig. 12, & text-fig. E 54 *t*). Their walls are minutely pitted (Pl. 3, fig. 11). The intermediary five to six layers of smaller cells still persist, though in a partially disorganized state, caught as they are between the sclerotic aqueous tissue and the lignified innermost layer of the inner integument.

It will be of help to consider in this connection some records that have been made in respect of the Capparidaceae. Baillon (1872) says that the innermost cell-layer of the integument of *Polanisia graveolens* produces a thin coat, which he called a third seed-coat and which covers the entire embryo in the ripe seed.

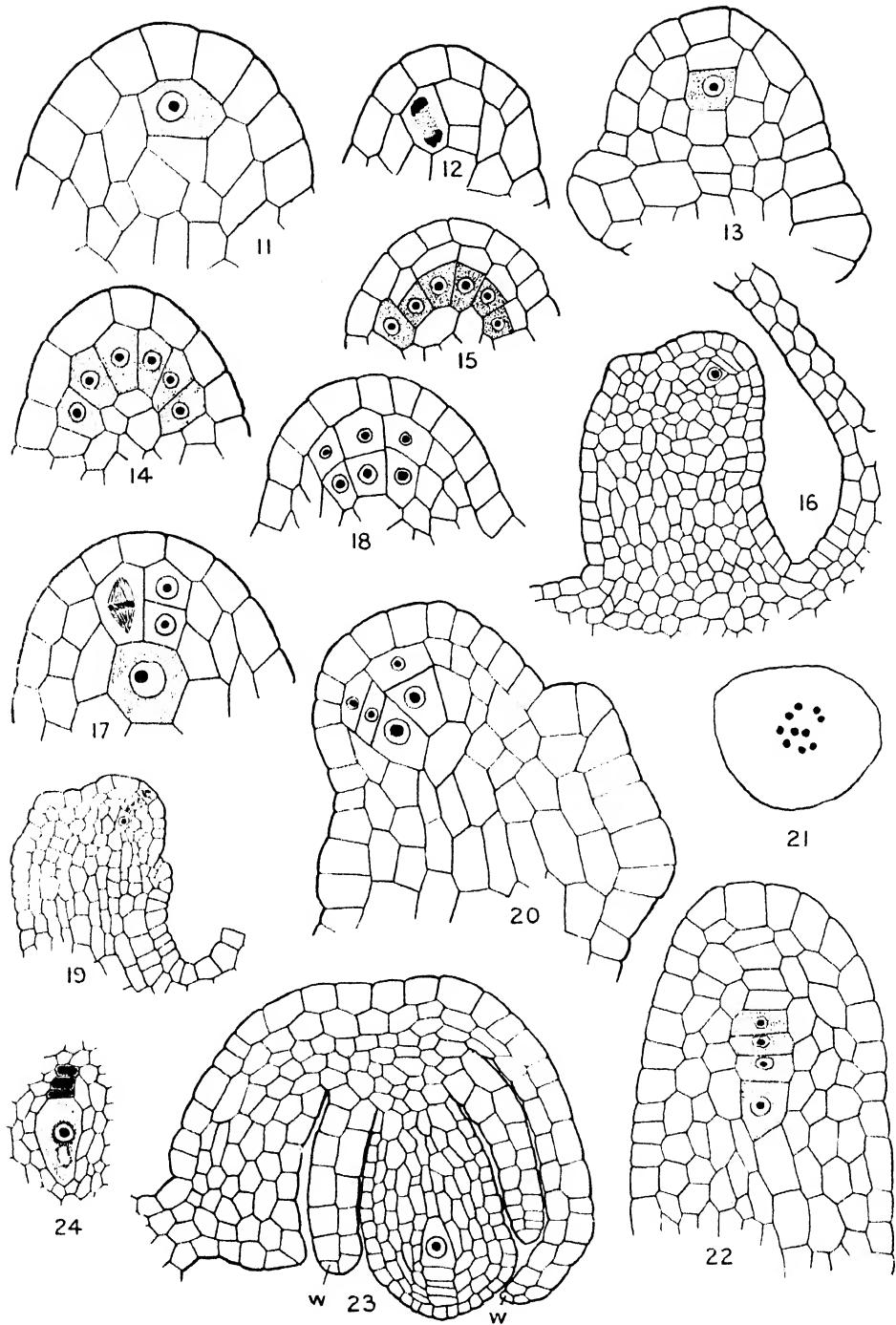


FIG. B.

Orr (1921 c) refers to this tissue as being adpressed to the inner wall of the testa, and its intimate relationship to the included embryo is emphasized by an infolding of the tissue between the radicle and the cotyledons. These layers, according to him, are composed of cells without protoplasmic contents, the walls of which are strengthened in various ways as seen in 'Oberflächenansicht' (Kuhn, 1928). Since these possess the form and structure of tracheids, this specialised layer is termed tracheal tissue. It is said to function first as an accessory water-supply system for the embryo (on account of its close association with the vascular strand of the funicle), and later to play an important part in the economy of the seed during germination, acting as a sponge, absorbing moisture through the micropyle, and constituting a kind of water-jacket surrounding the embryo. From a perusal of these accounts one gains the impression that one is dealing with a tissue that is secondary in its origin and which cannot in any way be related to the layers already constituting the integuments. Hence such names as third seed-coat and tracheal tissue have been given. Moreover, only surface views of these cells have been represented in Orr's (1921 d) paper. By following the ontogeny of the integuments from their inception to maturity, there can be no doubt as to the nature of the so-called third seed-coat. It is merely the enlarged cells of the innermost layer of the inner integument whose walls have become lignified. Pl. 3, fig. 11 of this paper represents the surface-view of the cells of this layer, and its identity with those of Orr (1921 d) can readily be recognized. Even in Orr's photomicrograph of the young ovule of *Isomeris* this layer can be recognized, lining, as it were, the nucellus of the ovule. Since no sections were taken of the mature seed and observations were confined to peels of the testa, it is likely that the mistaken impression was gained that the cells represented an additional tissue not already present.

THE OVULE.

As the young ovule grows outwards towards the wall of the ovary, it almost touches the latter (fig. B 16). The curvature is brought about by the rapid growth of the cells at the funicle and the chalaza, and this region subsequently forms what may be termed a raphe. The thick fibro-vascular tissue which connects the base of the nucellus with the placenta, the adherent funicle, does not attain the size and prominence of a Leguminous raphe, but is here of great interest in that during the post-fertilization campylotropous curvature it shows an inverted V-bend (fig. E 50, 51, 52). The ovule, after fertilization of the egg, shows a remarkable increase in size, and, this being more pronounced at the chalazal end, the funicle appears adpressed along the micropylar end of the ovule when the latter has attained its campylotropous form. Fig. E 48, 49, 50 show the course of development of the ovule from the anatropous state to the deeply lobed campylotropous condition. Fig. E 54, showing the micropylar portion of the young seed, reveals the fusion of the funicle completely with the outer integument. Mauritzon (1935) has shown in his figure of *Cleome*

violacea and *Polanisia* a similar fusion of the funicle with the micropylar end. According to him, a slight difference exists between the *Capparis* and *Cleome* types, for while in the latter there is this fusion, in the former the funicle issues out as a free cord without adherence either to the micropylar or to the chalazal end. While the inversion and the curvature of the ovule from an initial erect position seems to be common, as reported among others by Murbeck (1902) in *Ruppia*, Campbell (1897) in *Naias* and *Zannichellia*, and Joshi (1934) in *Digera*, the fusion of the funicle to the micropyle appears peculiar to the Cleomeae.

MEGASPOROGENESIS AND THE FEMALE GAMETOPHYTE.

When the archesporium is first distinguished, the ovule consists of a club-shaped mass of cells. It differentiates in the ovule even before the initiation of the integuments. Joshi (1934) has reported such an early differentiation in *Digera*. It also seems to be common in the Juglandaceae, where Langdon (1935) has reported it in *Carya* and *Juglans* and Woodroof (1928) in *Hicoria pecan*. Murbeck found it in the Rosaceae (1901) and Potamogetonaceae (1902). The primary archesporium consists of a single hypodermal cell (fig. B 11), but very often there are two or three cells (fig. B 18, 20). Occasionally a plate of hypoderms is seen to constitute the primary archesporium (fig. B 14), the cells of which could be readily recognised by their large size, prominent nuclei, and darker staining.

Multicellular archesporia have been reported in various genera distributed over a wide range of families. Strasburger (1879) was one of the earliest to report a multicellular archesporium, in *Rosa*. Coulter (1898) and Mottier (1895) recorded it in the Ranunculaceae. Guignard (1882) has observed two archesporial cells in *Capsella* and in *Aloe*. Conrad (1900) saw a mass of 20–60 cells manifesting an archesporial character in *Quercus*. Murbeck (1901) saw 'eine hypodermale Gruppe von Archesporzellen' in *Alchemilla*. Among the others, mention may be made of Ward (1880) in *Pyrethrum*, Frye (1902) in *Asclepias*, Maheshwari (1934) in *Ophiopogon*, Reeves (1930) and Martin (1934) in the Leguminosae, Chamberlain (1897) in *Salix*, Lloyd (1902) in Rubiaceae, and Puri and Singh (1935) in *Digera*. It thus seems to be common among the Archichlamydeae, especially the more primitive ones. Mauritzon (1935) has observed two archesporial cells in *Cleome spinosa*. Though in most multicellular archesporia previously recorded, only the median cell cuts off the primary parietal cell, here, as fig. B 15 indicates, all the cells of the archesporial plate have undergone periclinal division. Armour's (1906) figure 14 seems to indicate the cells of the 'sporogenous tissue' having divided periclinal in *Chloranthus*. Strasburger's (1897) plate 4, fig. 49, shows all the cells of the archesporial plate cutting off wall-cells in *Rosa livida*. In *Brassica oleracea* Pearson (1935) has observed that 'several archesporial cells lie beneath the epidermis of the ovule. These divide to form primary wall-cells and megasporangium mother-cells. The median one enlarges and the others are pushed aside'.

By the time the primary archesporium is differentiated in the ovule, the anther-sacs have advanced far in their development, the pollen tetrads being about to be organised. This shows decisive protandry of the flowers. The further behaviour of the primary parietal cell is rather irregular. Sometimes it divides anticlinally (fig. B 17). This is followed by further periclinal divisions by which the parietal tissue is added to. But more frequently it undergoes successive periclinal divisions (text-fig. B 16 & 19 ; Pl. 3, fig. 7). The parietals are very active from the time of their differentiation. In fig. B 19, which shows a row of four cells, the lowermost is the megasporangium mother-cell, while the upper three are the wall-cells. This could be easily mistaken for the linear tetrad, but that it is not is proved by the early stage of development the ovule is in, as indicated by the appearance of the primordia of the integuments. Fig. B 18 shows three juxtaposed archesporial cells having formed the parietals. Fig. B 20 shows also two archesporial cells, of which one has just cut off the parietal cell, while that of the other has already formed a periclinal wall. By the early activity of the parietals, six or seven layers of wall-cells are formed. Epidermal cells of the nucellus also divide (fig. B 19), so that there can be no doubt that the massive parietal tissue is built up of both the primary wall-cells and the epidermal cells of the nucellus. During all this interval the megasporangium mother-cell does not show any activity, except enlarging and keeping pace with the increasing mass of nucellar tissue, in which it ultimately becomes deeply set (Pl. 3, fig. 8, & text-fig. B 23). Heavy parietal tissue, and consequently a deeply embedded embryo-sac mother-cell, is considered to be a primitive character, being more prevalent among the families which are held to be phylogenetically primitive. Mauritzon (1935) has also made mention of this, and the *Capparis* type seems to have a greater amount of parietal tissue than *Cleome*.

It is interesting to note that, in almost all the families included under Centrosporae by Engler and Prantl (1891), there is a massive nucellus built up from both the primary parietal cell and the nucellar epidermis. Puri and Singh (1935) gave a list of all the genera of the Centrospermales which exhibit this feature. Nine chromosomes could be counted in each pole during heterotypic anaphase, but subsequent examination of pollen mother-cells in aceto-carmine has revealed the number to be ten (fig. B 21). The usual row of four megasporangia is formed, the upper three of which degenerate, while the lowest functions to form the enlarged embryo-sac (fig. B 22 & 24) in which the nucleus is situated in the middle, above a large vacuole. This nucleus soon enlarges and divides, the resulting daughter-nuclei migrating to opposite poles (fig. C 25) separated by a large central vacuole. The remains of the degenerated megasporangia are no longer visible. The nuclei undergo another division and the four-nucleate condition is attained (fig. C 26). In the meantime the embryo-sac enlarges considerably in size, and it seems that between the two-nucleate and the four-nucleate stages the increase in size of the embryo-sac is so great that its adult pre-fertilization size may almost be said to have been attained while yet it is

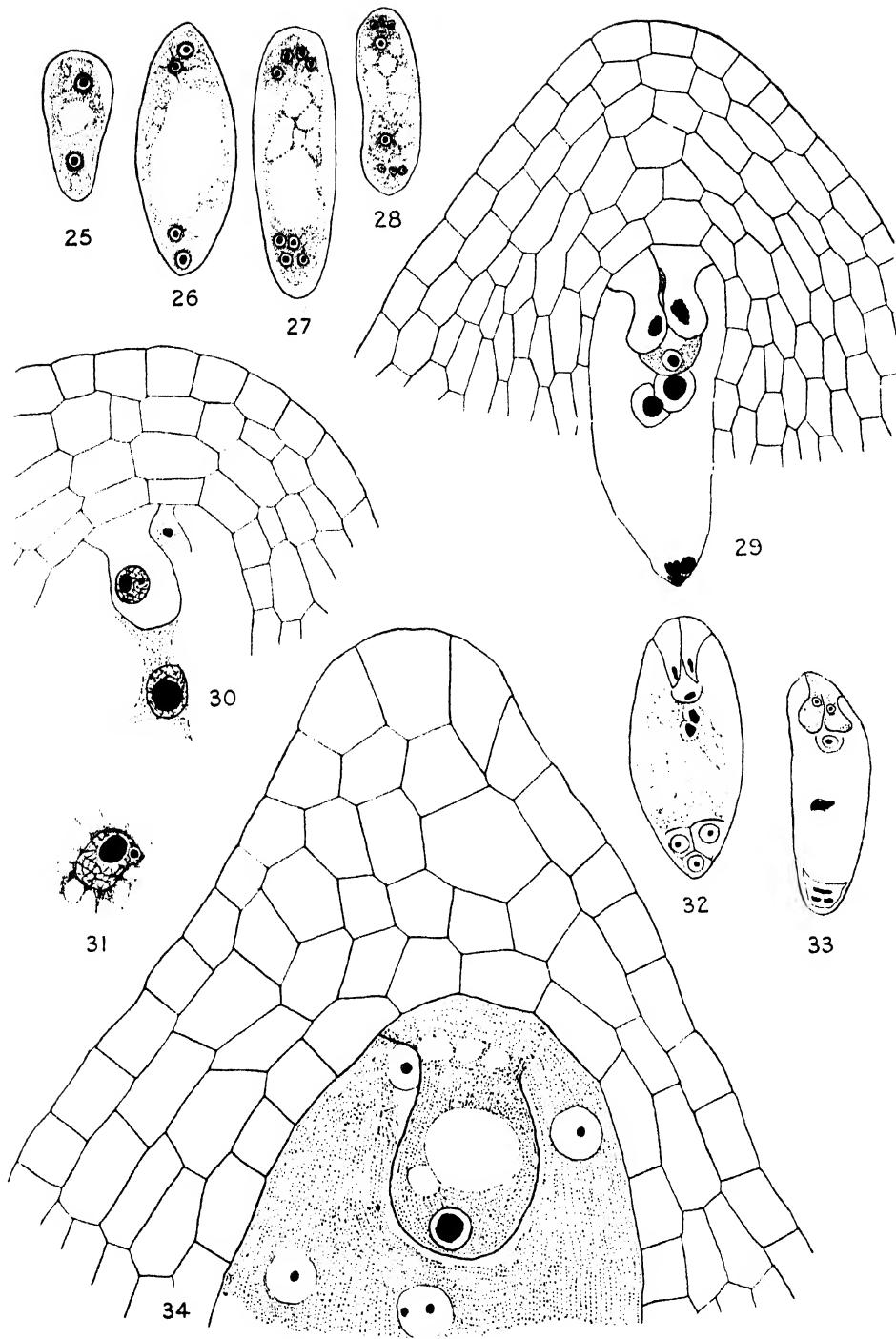


FIG. C.

in the four-nucleate stage. In other words, there is very little growth of the embryo-sac between the four-nucleate stage and fertilization.

By further division four nuclei appear at each end of the embryo-sac (fig. C 27). The polar nuclei, which can be easily distinguished quite early on account of their larger size (fig. C 28), migrate towards one another and meet just a little nearer the micropylar end (fig. C 29). Their actual fusion does not take place till just before fertilization.

The synergids are comparatively large, their nuclei often reaching the size of the nuclei of the oosphere. Their upper ends diverge very much, forming a hook-like curvature, so that they seem to hang like a drop from the micropylar wall of the embryo-sac (fig. C 29 & 33). This rather peculiar shape of the synergids, which Dahlgren (1928) terms 'hakenförmige Leistenbildung', has been observed by Mauritzon in *Gynandropsis*. He is of the opinion that 'diese Bildung im Pflanzenreich ziemlich allgemein ausgebreitet ist. Sie dürfte mit grösster Sicherheit in vielen Familien vorkommen, wo sie bisher nicht angetroffen worden ist, darauf beruhend, dass sie bei der Untersuchung übersehen worden ist'. Besides, this formation is not developed in younger synergids. Rao (1936) has recorded long and narrow synergids capped by the filiform apparatus in *Maerua*. Newman (1934) has described a 'hook or notch' in the upper part of the synergids of *Acacia Baileyana*. Dahlgren (1928) gives a list of plants in which the presence of the hook in the synergids had been recorded. He mentions no Capparidaceae; and he concludes that the notch is a characteristic structure, and not derived from plasmolysis and arises—'dürfte ihr entstehen allein von Entwicklungmechanischen Ursachen bedingt sein'.

The nucleus of the synergid is situated towards the upper end above a large vacuole (fig. C 33). In fig. C 29 & 32 the two synergids are degenerating, as shown by their nuclei, which are collapsing and have been pushed down by the vacuole. The egg may be below or beside the synergids. The egg also possesses this broadened basal portion (fig. C 30). The nucleus of the egg, which is much smaller than the fusion endosperm nucleus, is found towards the lower end of the cell, and above it is a big vacuole (fig. C 29). Fig. C 32 shows both the egg-apparatus and the fusion nucleus undergoing degeneration, while the antipodals can be seen to be organized into three cells, one at the bottom and two superimposed side by side at the base of the embryo-sac. The antipodals are usually insignificant and ephemeral, in contrast to the big antipodals observed by Rao (1936) in *Maerua*, where also they are said to degenerate before fertilization. The fusion endosperm nucleus is the biggest of all the nuclei in the embryo-sac. It assumes a position near the egg just before fertilization (fig. C 30).

FERTILIZATION.

Fertilization of the oosphere and of the endosperm nucleus was seen only in different ovules, and hence nothing exact can be said of the synchronology

of the two acts. The male nucleus is almost spherical. Vermiform and spiral shapes are said to be by far the commonest in Angiosperms. Guilliermond (1933) says that the male nucleus is generally vermiform and spiral. Spherical male nuclei have been only rarely reported. Mention may be made of the records by Weinstein (1926) in *Phascolus vulgaris*, Finn (1925) in *Asclepias cornuta*, Madge (1929) in *Viola odorata*, and by Newman (1934) in *Acacia Baileyana*.

Fig. C 30 shows the nucleolus of the male nucleus within the egg-nucleus, actual fusion not yet having taken place, and the remains of the degenerated synergids could be seen. In fig. C 31 the triple fusion of the embryo-sac is seen. It will be noticed that the male nucleus fusing with the fused polars is slightly bigger than that fertilizing the egg, as recorded by Thomas (1900) in *Caltha*, and also by workers mentioned above. Newman (1934) thinks that this is correlated 'with the longer period during which it is free in the embryo-sac'. The male nucleus as well as the egg-nucleus are in a resting condition at the time of contact. Besides Angiosperms like *Oenothera* (Ishikawa, 1918), *Vallisneria* (Wylie, 1923), *Cypripedium* (Pace, 1907), which show this condition of the male nucleus at the time of fusion, it is of interest that it is characteristic of the Coniferales (Guilliermond, 1933) and some Cycadales (Lawson, 1926). The triple fusion also takes place in the resting condition. Not much interval could, therefore, have elapsed between the two acts of fertilization, since both the male nuclei are in the resting stage.

THE ENDOSPERM.

Large-sized polar nuclei, of the kind occurring here, have been reported in a variety of families, among which may be mentioned those observed by Campbell (1897) in *Najas*, Gupta (1934) in *Potamogeton*, and Woodroof (1928) in *Hicoria*. Migration of the polar nuclei towards the egg-apparatus has been recorded in *Melilotus* by Cooper (1933) and in *Daucus* by Borthwick (1931). The division of the triple fusion nucleus takes place soon after fertilization, but long before division of the oospore. This feature seems to be common, especially in the Leguminosae (Weinstein 1926, Martin 1914, and Maheshwari 1931). A number of free nuclei are formed and lie in the protoplasm which lines the embryo-sac. These are distributed as a simple layer along the wall of the embryo-sac, but a denser layer of cytoplasm collects about the oospore, where the nuclei form several layers. The centre of the sac contains a vacuole which as the embryo-sac rapidly increases in size displaces the surrounding nucellus, though not entirely. The multinucleate endosperm becomes cellular at a late stage, when the sac has reached its maximum size and at which time the embryo is about to enter upon the stage of lobing of the cotyledons. In fig. E 54, which shows the octants of the embryo cutting off dermatogen cells, the endosperm nuclei were in a state of division. They divide more or less simultaneously. The wall-formation, however, is not simultaneous throughout the embryo-sac. It begins around the embryo and is basipetal. On account

of this, some of the cells at the periphery of the chalazal end of the sac contain two or three nuclei each, the wall-formation having not yet taken place.

In *Colutea* (Nemec, 1910) it was found that the peripheral nuclei of the chalaza increased in size and became lenticular. Wall-formation began in the micropylar region, but it stopped half-way, the chalazal nuclei remaining unsurrounded by walls. How far the condition found in *Cleome* can be considered as leading to the condition of non-cellular endosperm, such as exists in the Sympetalae, through some stage as represented by *Colutea*, can be determined only after the study of more forms.

A fully developed endosperm cell is polygonal (fig. D 47), and has a prominent nucleus with a number of starch grains in the cytoplasm.

THE EMBRYO.

The development of the embryo begins with an enormous increase in the size of the oospore. Above the zygote nucleus is a large vacuole (fig. C 34). The first division of the zygote is by a transverse wall (fig. D 35), and this takes place five to seven days after pollination. It is during this interval that the ovule, and with it the embryo-sac, undergo not only great enlargement, but also the campylotropous curvature. Of the two resulting cells, the upper constitutes the basal cell (*b*) and the lower, the terminal cell (*t*) (fig. D 35). Even from the start, the basal cell which ultimately forms the suspensor, is bigger than the terminal which is to generate the embryo proper. (*b*) divides transversely into two cells (*c* & *d*), while simultaneously the terminal cell (*t*) undergoes longitudinal septation (*t*₁ & *t*₂). This four-celled pro-embryo thus formed consists of three tiers of cells (fig. D 36), the upper two superimposed and the lower juxtaposed, and this according to Souéges (1918, 1919) is a very important stage since each of these cells gives rise to a definite region in the mature embryo, and the method is considered to be the same in all members of each family or group. The arrangement of the cells in the four-celled pro-embryo would appear to fall into two main types, in one of which all the four cells are arranged in a linear series, while in the other the upper two are one over the other and the lower two lie side by side. The former is characteristic of families like Rubiaceae and Solanaceae (Souéges, 1922, 1924), Leguminosae (Cooper 1933, Weinstein 1926), and Umbelliferae (Borthwick, 1931). The latter is found in Cruciferae, Ranunculaceae, etc. (Souéges, 1913, 1919).

Of the two cells *c* and *d*, the one attached to the micropylar end *c* is bigger and soon suffers transverse septation into two cells, *c*1 and *c*2, of which *c*1, the uppermost, is bigger, and comes to assume a large hypertrophied appearance (fig. D 37, *c*1). This *c*1 again divides transversely, cutting off a large basal cell *c*1/1, and a smaller cell *c*1/2 below it, while *c*2 divides likewise into three cells *c*2/1 ; *c*2/2 ; and *c*2/3 (fig. D 38).

At about this time *d* divides transversely into *d*1 and *d*2, of which the lower *d*2, being next to the embryonal sphere, functions as the hypophysis. Fig. D 38 shows the cell *d* still in an undivided condition, while fig. D 40 represents the

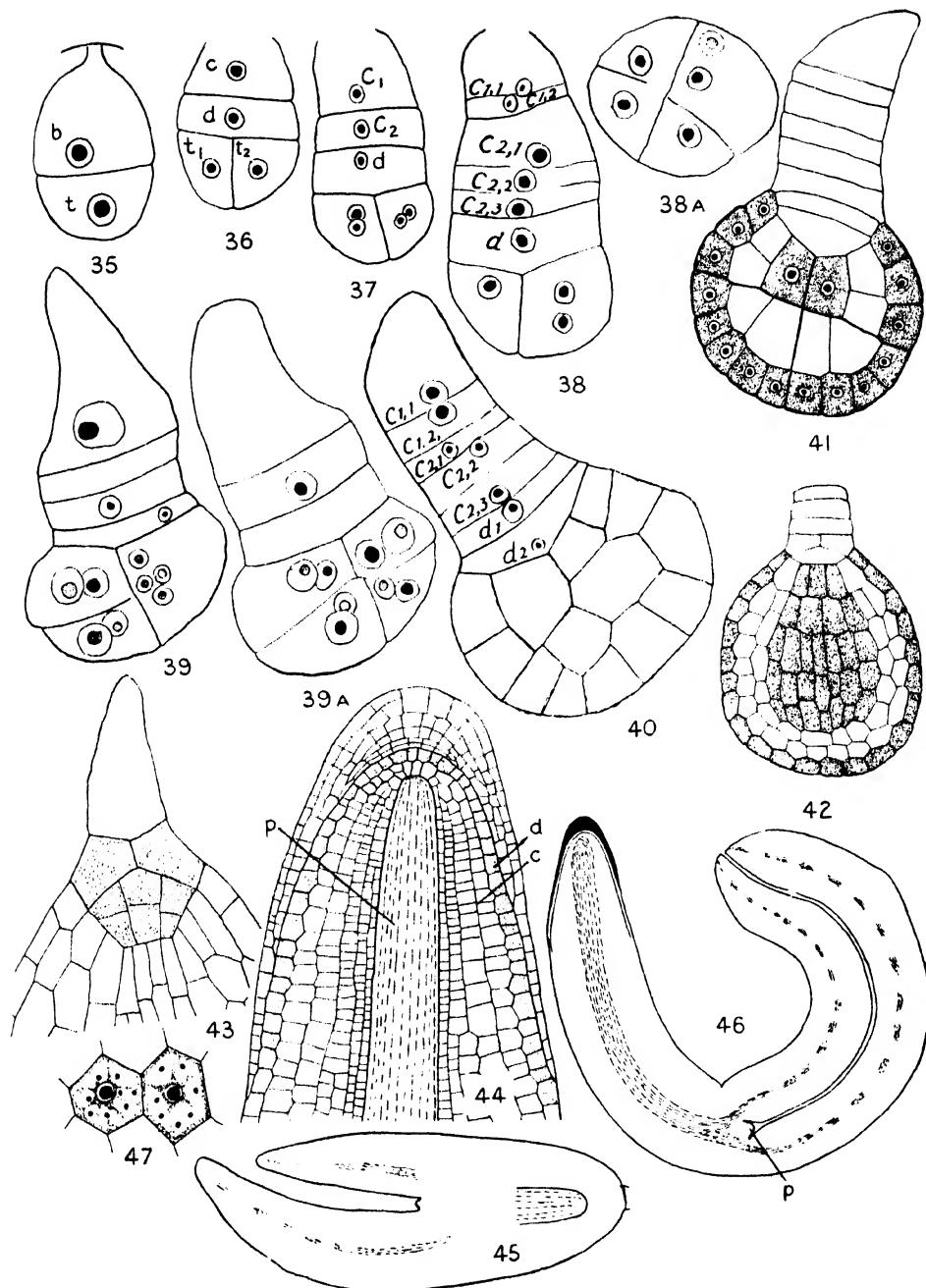


FIG. D.

complete suspensor organized. It consists of seven cells, of which the lowest functions as the hypophysis. Of these seven, the five basal ones $c1/1$; $c1/2$; $c2/1$; $c2/2$; and $c2/3$ are derived from c of the four-celled pro-embryo, while d has contributed only two cells to the suspensor, of which one acts as the hypophysis.

It is interesting at this stage to compare this suspensor and its derivation with that of *Capsella*, not only because *Capsella* is held to be the type for Dicotyledonous embryo-formation, but because it belongs to a family closely allied to the Capparidaceae.

The formation up to the four-celled stage is the same as for *Cleome* (Souéges, 1919). The basal cell ci divides into two, g and v , of which the one attached to the micropylar end (v) is larger and vesicular. By another transverse septation, g gives rise to m and n . In the meantime, the intermediary cell (cm) of the four-celled pro-embryo divides by two successive divisions into a row of four cells (p , q , r , & s). The cell p nearest the embryonal sphere divides into h and j , of which h is the hypophysis. The cell next to p , that is q , divides into k and l , while r and s do not further divide. Thus, including the hypophysis, there are nine cells constituting the suspensor, though it must be mentioned that this is not a fixed number, as Souéges (1919) himself says that he has found eleven in not a few instances. Of these nine cells, the six distal cells have been formed by the intermediary cell (cm) of the four-celled pro-embryo, and the basal three by the original basal cell (ci). Thus not only is there a patent difference between the two in respect of the ultimate increased length of the suspensor, brought about in *Capsella* by the larger number of cells and the great swelling of the basal vesicular cell, but also in the manner of derivation of the suspensor as a whole. In *Capsella* six of the nine cells have been derived from the intermediary cell, while the basal contributes only three, including the large vesicular cell. In *Cleome* almost the reverse happens, the intermediary cell d dividing but once to form the hypophysis.

In *Ranunculus sceleratus*, Souéges (1913) has indicated that the middle cell h functions directly as the hypophysis, without contributing anything to the formation of the suspensor. Whether the type of hypophysis formation in *Cleome* represents an advance over that in *Ranunculus*, leading to the *Capsella* type, can be seen only after ascertaining its prevalence or otherwise in the family as a whole.

The fate of the terminal cell t can now be considered. Another longitudinal wall laid down at right angles to the first initiates the quadrant stage (fig. D 37). A transverse wall across the quadrants gives rise to the octant stage of the globular embryo, in which the primordia of the cotyledonary and the hypocotyledonary regions are differentiated. Fig. D 38 and 38 *a* show transverse, as well as longitudinal, views of the octants. Figs. 39 and 39 *a* show the two halves of an embryo cut obliquely lengthwise at the sixteen-celled stage. Walls laid parallel to the periphery in each of these cells separate rudiments of the dermatogen of the epicotyl and the hypocotyl (fig. D 40, 41). While these

outer cells multiply by radial divisions, the inner mass of tissue grows in all directions, resulting at an early period in its differentiation into plerome and periblem of the root (fig. D 41). The mass of tissue increases rapidly by the multiplication of the cells, and the cotyledonary protuberances are soon initiated. It is only at a slightly later stage that the rudiments of the plerome of the cotyledons become distinguishable within each cotyledonary lobe. This grows with the cotyledons (fig. D 45), whose entire length it traverses, and in the mature embryo (fig. D 46) the two plerome strands of the two cotyledons converge and meet the plerome of the root in the hypocotyledonary region. The posterior or the basal end of the axis of the embryo, after the differentiation of the primary meristems into dermatogen, plerome, and periblem, is, as it were, incomplete as long as this differentiation has not also taken place in the hypophysis. The hypophysis divides into two cells, one over the other, of which the lower arches into the embryonal sphere (fig. D 41). Vertical wall-formation then takes place, after which the lower two break up into two layers, of which the outer becomes continuous with the dermatogen of the axis, while the inner forms a prolongation of the periblem (fig. D 43).

The peripheral dermatogen, which elsewhere remains simple, increases in thickness at this region, where it covers the apex of the root and functions as the calyptrogen. This is secured by repeated tangential divisions. Of the two layers that are thus successively formed at each of these divisions, the outer becomes the layer of the root-cap, while the inner remains as dermatogen and repeats the process. A fully mature embryo (fig. D 46) has a deeply curved appearance, the hypocotyledonary portion including the radicle and the cotyledons being more or less of equal length. Between the cotyledons is enclosed the plumule (*p*), which looks like a small papillate protuberance. The lobing of the cotyledons takes place on the thirteenth or the fourteenth day after pollination. The ovule reaches its maximum size then; the fruit at this stage is about 6·2 cm. long. The seed is fully mature about forty days after pollination.

THE NUCELLUS.

That there is a massive nucellus has already been indicated. When the embryo-sac is ready for fertilization, it occupies, as is shown in text-fig. A 9, only a small portion of the nucellar tissue. In *Polanisia griseolens* Guignard (1893) found that the embryo-sac at the time of fecundation occupied but a third of the nucellus. Mauritzon (1935) found one to two layers of cells between the embryo-sac and the nucellar epidermis in the *Cleome* type, which after fertilization degenerate so that the embryo-sac comes to lie close to the epidermis. It is only in *Capparis frondosa* that he found about four layers persisting up to a late stage, some of which help in the development of nucellar embryos. In *Cleome Chelidonii*, however, four to six layers of cells separate the embryo-sac from the nucellar epidermis for quite a long time. In fig. C 34, representing an advanced zygote long after fertilization, there are about five layers present.

An examination of the mature seed reveals the definite presence of a few layers of tissue surrounding the entire embryo, and this is more in the recessed part of the ovule, as also in the micropylar region capping the radicle (fig. E 53 and Pl. 3, fig. 13). I have examined the seeds in different stages of development, and have seen that the enlarging embryo-sac with the included endosperm does not absorb the entire nucellar tissue, but a definite portion remains unused surrounding the developing embryo. This persistent tissue in the mature seed is therefore regarded as of the nature of perisperm, the cells of which have undergone slight modification to serve as a storehouse ; they look very much like the peripheral cells of the cotyledons.

Guignard (1893) has insisted on the constant presence in the interior of the integument of certain layers of cells derived from the albumen which often alter in shape, not only in the Cruciferae, but also in the Capparidaceae and Resedaceae, and he thinks that such seeds should not be called exalbuminous. Of *Polanisia graveolens* he says that the tissue of the nucellus is absorbed almost entirely on the face of the convex side of the seed, but there are left a few layers on the concave side. The albumen is said to act in the same way, without always reducing itself to the same degree, principally in the micropylar region, where it forms a 'mauchon' round the radicle of the embryo. Baillon (1872) remarks that the seed of *Capparis spinosa* encloses a small quantity of albumen in the numerous foldings of the irregularly folded embryo. Mauritzon (1935) states that there is a quantity of nucellus even at such a late stage as the lobing of the cotyledons. He was not able to examine older seeds, but suggests the possibility of its persisting as perisperm.

The tissue in question is either endosperm or perisperm, or a new tissue secondary in its origin, being derived from the integumental layers. It has been noted that quite early in the life of the ovule the cells of the innermost layer of the inner integument become larger and their walls lignified (fig. E 54, t), and this in the mature seed persists as the 'tracheal tissue', enveloping the embryo. It is not therefore likely that this could have divided and formed a secondary tissue.

Fig. E 52, representing the ovule at the time of formation of the cellular endosperm, at which stage the cotyledonary lobing of the embryo has just taken place, reveals the undoubted presence of a definite unused nucellus. According to Goebel (1887), the time of formation of the cellular endosperm marks the cessation of the growth of the embryo-sac. In other words, the ovule reaches its adult size, and beyond that stage there is no further increase in size of either the ovule as a whole or of the hitherto developing embryo-sac with the endosperm tissue in it. It is only the embryo that begins to enlarge at the expense of the surrounding endosperm. So what is seen as definite nucellar tissue at this stage cannot hereafter disintegrate, as this would involve its absorption by the embryo-sac with a consequent increase in its size. It is therefore held that the tissue that surrounds the embryo in the mature seed represents only the modified cells of this original nucellus and, as such, it is

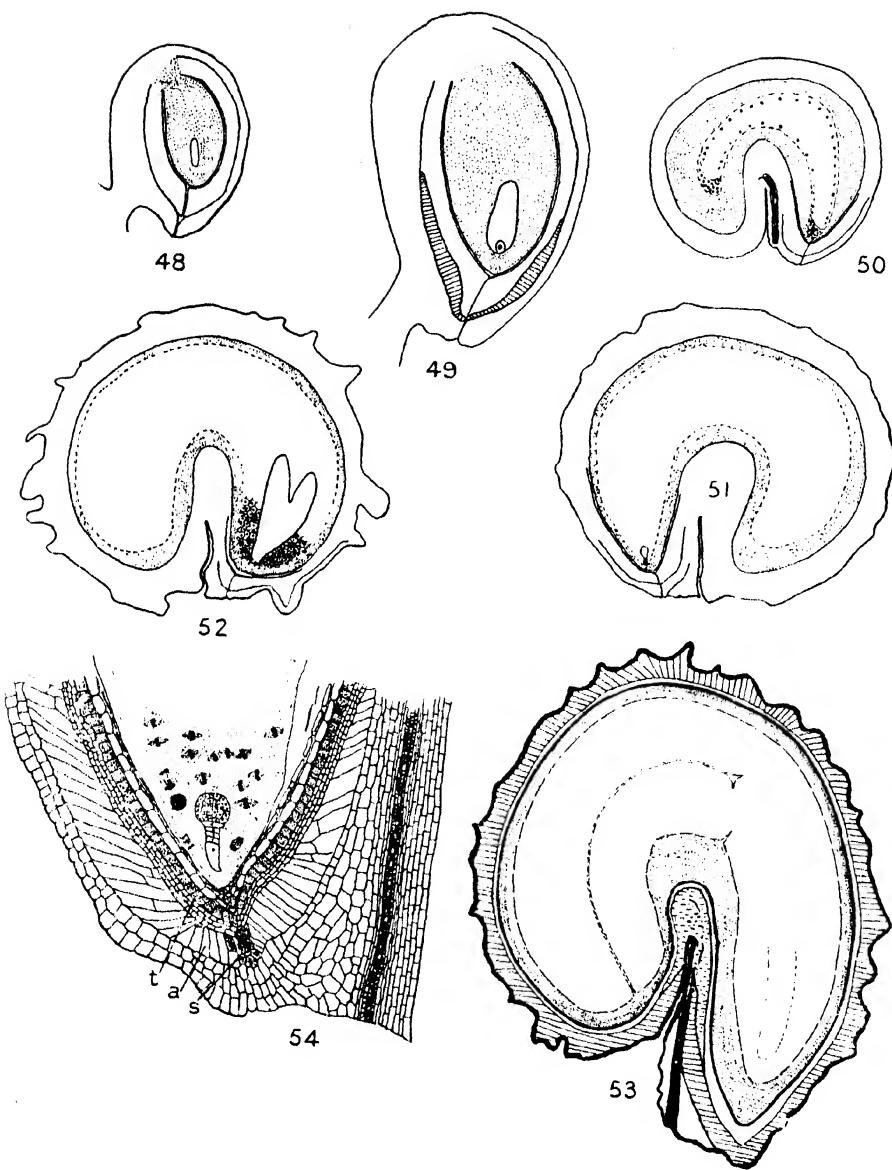


FIG. E.

to be regarded as perisperm. At one time I wondered if this tissue could possibly be identical with the tracheal tissue of Orr (1921 c). The absence of any lignified markings on the walls of the cells, however, and the presence of food-reserves in the form of starch-granules and oil-globules rule out such a possibility. Moreover, it has been shown above (p. 52) that the tracheal tissue is not really a third integument as believed by Baillon (1872) and Orr (1921 c), but merely the greatly lignified cells of the innermost layer of the inner integument.

NUCELLAR 'STRANDS'.

Pl. 3, fig. 10 (b), and text-fig. A 9 reveal the presence of elongated cells with distended and perhaps disintegrating nuclei from the base of the embryo-sac to the chalaza. These cells are quite distinct from the rest of the cells of the nucellus and also from the usual degeneration area which often is present surrounding and sometimes below the sac. Frequently longish cells are present below the megasporangium mother-cell in the young ovule. Pl. 3, fig. 9 (b) shows the megasporangium mother-cell situated at the top of an axial row of cells. Benson (1893) has recorded the presence of a central series of coaxial strands which are said to be sporogenous in *Fagus*. Sometimes there is a tendency to develop one strand more prominently than the rest. Fig. 5 of her paper is almost identical with that of Pl. 3, fig. 9. Ward (1880), describing the development of the ovule in *Batomus*, says that there is regularity of arrangement of the constituent cells, which becomes better expressed at a little later stage as an axial row of cells. Later the terminal cell of this series becomes larger and forms the embryo-sac mother-cell. His pl. 17, fig. 4 is almost identical with Pl. 3, fig. 9. In later stages (*cf.* his pl. 18, fig. 1) he represents these elongated cells of the axial row at the base of the embryo-sac and connecting it with the vascular bundle of the funicle. Benson (1893) has observed tracheids at the base of the embryo-sac of *Castanea*. After careful examination I am of the opinion that the central axial strand of *Cleome* is not sporogenous, except the megasporangium mother-cell at the top, and believe that it is these cells that later constitute the elongated degenerating cells connecting the base of the embryo-sac with the chalaza. Of the vasculation of the ovule as a whole, Schnarf (1931) says that more rarely than in the integuments there has been found some sort of vascular strands in the nucellar region of the Capparidaceae, Thymelaeaceae, etc. Besides, in *Castanea* referred to above, nucellar tracheids have been reported by Treub (1891) in *Casuarina*; Frye (1902) saw a single tracheid in *Asclepias Cornuta*. Orr (1921 a) has observed the presence of elongated elements with well-defined annular thickening on their walls in the nucellus of many of the ovules of *Steriphoma Cleomoides*, occurring singly or in groups. In *Cleome Chelidonii* no tracheids in the strict sense of the term have been detected, inasmuch as no thickenings of any kind have been found. But the definite presence of these elongated cells with degenerating nuclei and walls does suggest that they are to be regarded as the vestiges of a conducting tract. That tracheids occur in another Capparidaceous genus, *Steriphoma*, strengthens

this belief. Orr (1921 a) admits that it is not possible to say whether these play a definite part in the economy of the ovule or are merely survivals of a primitive feature traceable to the vascular sporangia of a long extinct ancestor. It is not surprising that in a form such as this, where there is a massive nucellus and where the embryo-sac, even after attaining its eight-nucleate condition, occupies but a fraction of the nucellar tissue, means should exist to facilitate translocation of food and water from the placental strands to the remote enlarging embryo-sac.

These nucellar vascular strands may not have much phylogenetic significance, since an isolated tracheid has been found in such an advanced family as the Asclepiadaceae (Frye, 1902); but their wider distribution in such families as the Amentiferae, Thymelaeaceae (Schnarf, 1931), and the Capparidaceae seems to indicate the necessity of its being stamped a primitive feature. Newman (1934) mentions the presence of a column of elongated cells below the antipodal pocket and connecting the vascular bundle of the ovule with the embryo-sac of *Acacia Baileyana*.

The presence of the aqueous tissue and the tracheal sheath as specialized structures of the inner integument, and of the nucellar strands in the young ovule, point to an efficient mechanism for the conduction and conservation of water as existing in the economy of the ovule and the seed of the Capparidaceae. Both, however, may be the relies of a more complex water-storage and conducting system.

SUMMARY.

1. A historical survey is made of the Capparidaceae and the genus *Cleome*, and the life-history of *Cleome Chelidonii* is described especially as regards the female gametophyte, embryo, and seed-development.
2. The floral organs arise in acropetal succession, and the carpels are lateral in origin.
3. The ovule is anatropous till fertilization, after which there is a great enlargement coupled with a curvature, resulting in the campylotropous form, the funicle becoming fused with the micropylar side.
4. The outer integument completes its development earlier than the inner, and the micropyle is not straight.
5. The tracheal sheath surrounding the embryo, which was supposed to be a third integument, is proved to be the innermost layer of the inner integument. The development of aqueous tissues consisting of long columnar cells with lignified striations from the outermost layer of the inner integument is recorded and compared with *Gnetum*.
6. A row of elongated cells with degenerating nuclei and walls at the base of the embryo-sac are held to represent vestiges of a once-functional nucellar strand, and the analogy with the Amentiferae is pointed out.
7. The archesporium of the ovule is hypodermal, consisting of either a single cell or a plate of cells.

8. A massive parietal tissue is formed by the division of both the primary wall-cell and the cells of the nucellar epidermis.

9. The chromosome number is $n=10$, counts having been made on acetocarmine preparations of PMC.

10. A normal eight-nucleate embryo-sac is formed. The synergids possess the 'hakenförmige Leistenbildung' at their base, and the antipodals are ephemeral.

11. The endosperm fusion nucleus is just below the egg at the time of fertilization, and is much bigger than the latter.

12. The male nuclei are spherical and fusion takes place with the egg and endosperm nucleus while they are in a resting condition.

13. The triple fusion nucleus divides earlier than the zygote.

14. A suspensor of about seven cells is ultimately formed. The hypophysis is derived by a single division of the intermediate cell of the four-celled pro-embryo, and it is suggested that this is a condition intermediate between the Ranunculaceae and the *Capsella* type.

15. The presence of perisperm surrounding the mature embryo is recorded.

In concluding this part of the work, I wish to express my thankfulness to the Vice-Chancellor and the Syndicate of the Annamalai University for the award of the Foreign Fellowship, the holding of which has rendered this work possible. To Professor Ruggles Gates, F.R.S., under whom the work was carried out, it is a pleasure to express my sincere gratitude for the many valuable suggestions and help that I have received at his hands.

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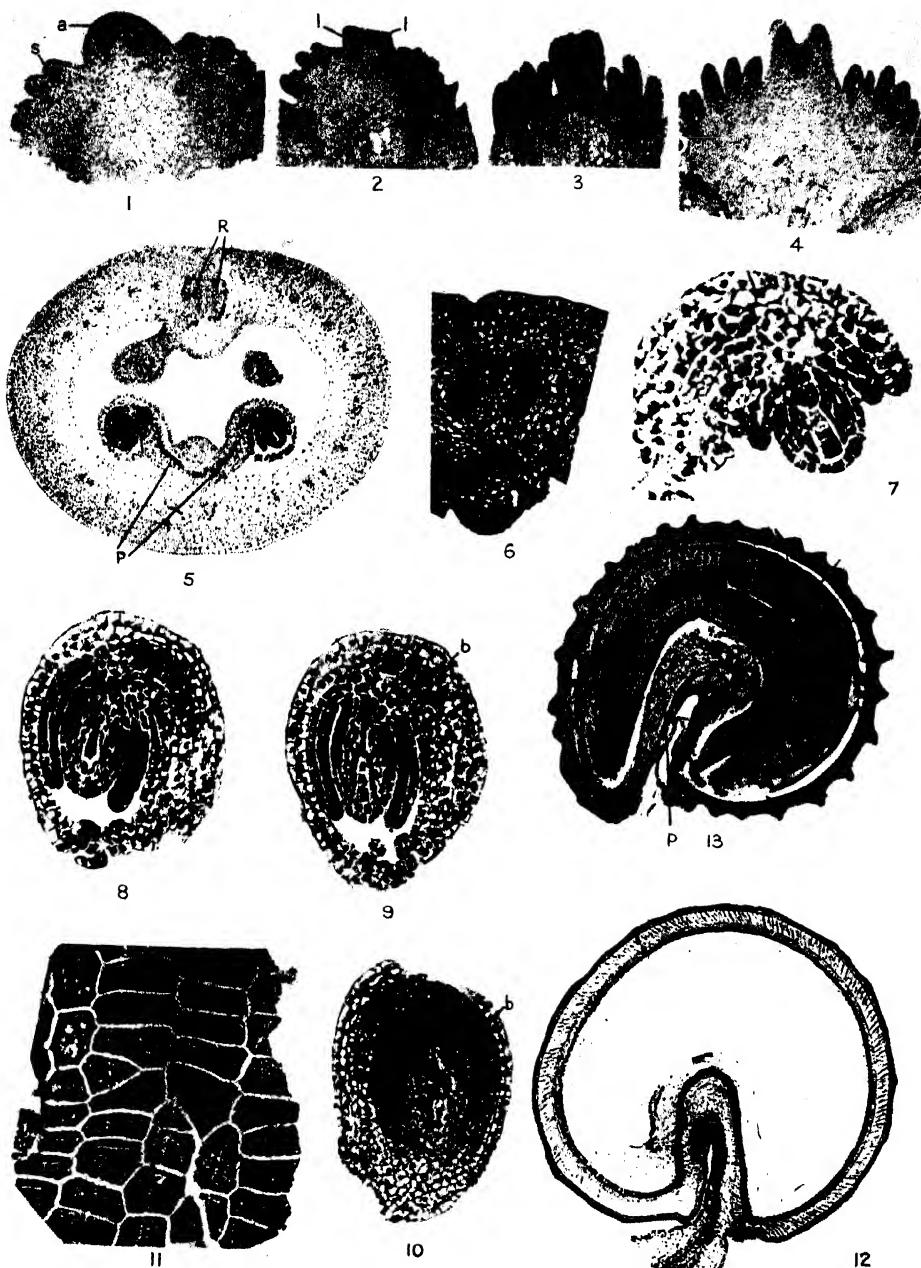
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EXPLANATION OF PLATE 3 AND TEXT-FIGURES.

All the text-figures have been prepared from camera-lucida drawings. Plate 3 consists of photomicrographs reduced by a quarter.

PLATE 3.

Fig. 1. Longitudinal section of floral apex. From the broadened disc that surrounds the apical dome (*a*) the stamen primordia are seen to arise (*s*). $\times 37\cdot5$.

Fig. 2. A slightly later stage, showing the lateral initiation of the carpel primordia (*l*) from the domed apex. $\times 25$.

Figs. 3 & 4. Still later stage ; the apex of the dome and the two lateral carpel primordia are seen as three distinct deeply staining regions. $\times 25$ and $\times 37\cdot5$ respectively.

Fig. 5. Transverse section of ovary with ovules, in which the outer integumental halves are fully grown. The absence of any well-defined mid-rib in the valves and the double nature of the commissural bundles (*R*) are shown. *P* represents the placental strands. $\times 25$.

Fig. 6. Commissural region of an older ovary. The two vascular bundles and the depression between them are seen. $\times 45$.

Fig. 7. The archesporial cell has cut off four parietal cells by successive periclinal divisions. $\times 95$.

Fig. 8. The megasporangium mother-cell still undivided and embedded in a heavy parietal tissue. $\times 70$.

Fig. 9. The megasporangium mother-cell at the head of an axial strand of cells (*b*). $\times 70$.

Fig. 10. The fully formed micropyle and the elongated cells at the base of the embryo-sac (*b*) forming the 'nucellar strands'. $\times 50$.

Fig. 11. Surface-view of the cells of the tracheal sheath showing pits on their walls. $\times 137\cdot5$.

Fig. 12. Ovule showing the fusion of the funicle with the micropylar side, the funicular strand showing an inverted V-bend. The aqueous tissue as a specialized layer of the inner integument is seen surrounding the whole embryo-sac. $\times 17\cdot5$.

Fig. 13. Vertical section of mature seed showing the presence of perisperm (*p*) surrounding the embryo. $\times 12\cdot5$.

TEXT-FIGURE A (p. 47).

1. Floral diagram at a very young stage of the flower, showing the median pair of sepals as the outer and also the origin of the glandular hairs on the dorsal surface of the sepals. $\times 30$.
2. Superficial origin of the integumental primordia. *oi.*, represents the enlarged epidermal cell from which the dorsal half of the outer integument arises. *ii.*, the inner integumental initial has already divided. $\times 600$.
3. Oblique wall-formation in the superficial initial and the cutting off of the wedge-shaped apical. $\times 600$.
4. An example of radial wall-formation preceding oblique wall-formation of the initial. $\times 600$.
5. A portion of the inner integument at the linear tetrad stage. The inner layer has divided to form three layers of cells. The wedge-shaped apical *w* is also shown. $\times 600$.
6. Inner integument at a later stage. The wedge-shaped cell has divided in an irregular manner to form a massive apical region. The cells of the middle layer of the three-layered integument have divided more or less simultaneously. $\times 400$.
7. The origin of the spinous outgrowths in the testa, by the radial elongation of the cells of the outer layer of the outer integument. These become suberized. The cells of the aqueous tissue derived from the outermost layer of the inner integument showing the scalariform markings. The innermost layer of the inner integument which is the tracheal sheath and the intermediary four or five layers of soft-walled cells are also shown. $\times 400$.
8. A stoma from the outer wall of the ovary. $\times 600$.
9. Embryo-sac at fertilization occupying but a portion of the nucellus. The nucellar strand is visible at the base of the embryo-sac. The sclerotic cells (*s*) and the aqueous tissue (*a*) which originate as specialized regions of the inner integument at the micro-polar region merging with one another. *t* is the tracheal sheath, being the innermost layer of the inner integument. $\times 100$.
10. A few cells of the aqueous tissue showing their largely vacuolated nature and the persistence of the cytoplasmic contents. $\times 600$.

TEXT-FIGURE B (p. 51).

11. A single hypodermal cell constituting the archesporium of the ovule. $\times 600$.
12. The archesporial cell at late anaphase. $\times 600$.
13. The archesporial cell cutting off the primary parietal cell. $\times 600$.
14. Hypodermal plate of archesporial cells. $\times 600$.
15. All the cells of the archesporial plate cutting off parietal cells. $\times 600$.
16. The beginning of the curvature of the ovule by which it almost touches the wall of the ovary. Two parietal cells have been formed by successive periclinal divisions. $\times 400$.
17. The first division of the primary parietal cell is anticlinal. One of the daughter-cells has already divided by a periclinal wall, while the other is in metaphase. $\times 600$.
18. Three juxtaposed archesporials all having cut off parietals. $\times 600$.
19. Three parietals being formed by successive periclinal divisions with the megasporangium beneath them simulating linear tetrad. The epidermal cell of the nucellus is also in a state of division. $\times 400$.
20. Two juxtaposed archesporials, one of which has formed two parietals by two tangential divisions, while the other has just formed the primary wall-cell. The initiation of the integuments is also seen, the inner slightly earlier than the outer. $\times 600$.
21. Metaphase I (polar view) of pollen mother-cell. $\times 1800$.
22. Linear tetrad, the lowest being the functioning megasporangium. $\times 600$.

23. An ovule showing the overtaking of the inner integument by the outer, each with its wedge-shaped apical cell (*w*). The megasporangium is greatly enlarged and is embedded in a massive nucellus. Four or five layers of wall-cells have been formed. $\times 400$.
24. The degenerating megasporangium with the functioning megasporangium enlarged. There is a vacuole beneath the nucleus. $\times 600$.

TEXT-FIGURE C (p. 55).

25. Binucleate embryo-sac, a large vacuole separating the two nuclei. $\times 600$.
26. Four-nucleate embryo-sac with the vacuole greatly enlarged. $\times 600$.
27. Eight-nucleate embryo-sac with four nuclei at each pole. $\times 600$.
28. The polar nuclei are bigger than the rest and are beginning to migrate towards one another. $\times 600$.
29. A fully formed embryo-sac with the egg-apparatus organized. The nuclei of the synergids have degenerated, and the 'hakenförmige Leistenbildung' as also the vacuole above the egg-nucleus could be seen. The antipodal cells have also degenerated, while the polars have not yet fused and have taken up a position at the base of the egg. Five to six layers of cells separate the embryo-sac from the nucellar epidermis. $\times 600$.
30. Fertilization of the egg. The bigger nucleolus is that of the oosphere, the smaller is that of the male nucleus. The endosperm fusion-nucleus and the remains of one of the synergids are also seen. $\times 600$.
31. Triple fusion. The spherical nature of the male nucleus and its being in the resting condition at the time of contact could be seen. $\times 600$.
32. Embryo-sac in which the egg-apparatus and the polar nuclei have degenerated, while the antipodal cells are organized into three distinct cells. $\times 600$.
33. Embryo-sac with the egg-apparatus well organized. The vacuoles below the nuclei of the synergids are seen. $\times 600$.
34. Oospore with a large vacuole above the nucleus and a few free endosperm nuclei distributed around it. About five layers of cells separate the embryo-sac from the nucellar epidermis. $\times 600$.

TEXT-FIGURE D (p. 59).

35. The oospore divided into two cells by a transverse wall into the basal cell (*b*) and the terminal cell (*t*). $\times 600$.
36. The four-celled pro-embryo in which the terminals *t* 1 and *t* 2 are juxtaposed. $\times 600$.
37. Embryo at quadrant stage. *c* has divided into *c* 1 and *c* 2. $\times 600$.
- 38 & 38 A. Octants cut obliquely. *c* 1 has divided into *c* 1/1 and *c* 1/2, while *c* 2 has formed *c* 2/1, *c* 2/2, and *c* 2/3, while *d* has remained undivided. $\times 600$.
- 39 & 39 A. Each of the octants has divided once to form the sixteen-celled stage. $\times 600$.
40. The full suspensor of seven cells is formed by the division of *d* into *d* 1 and *d* 2 and the latter arches into the embryonal sphere functioning as the hypophysis. $\times 600$.
41. A slightly later stage in which tangential walls have differentiated the dermatogen and the plerome, both of which are shown shaded. $\times 600$. The hypophysis *d* 2 has divided into two by a transverse wall.
42. A still later stage where the dermatogen, periblem and plerome have become distinguished, the first and the last being represented shaded. $\times 300$.
43. Hypophysis (shaded) divided first by a transverse wall and then by longitudinal walls; the outer layer becomes later on continuous with the dermatogen and the inner with the periblem. The cells of the suspensor at this stage have lost their individuality and their nuclei are degenerated. $\times 400$.

44. Tip of radicle showing origin of root-cap. *p*, plerome, *d*, dermatogen, and *c*, periblem. $\times 200$.
45. Cotyledonary lobes at an advanced state of development. The rolling of the cotyledons in conformity with the campylotropy is initiated by the outer cotyledon becoming bigger and commencing to roll up. The plerome of the root and that of the cotyledons are indicated by dotted lines. $\times 100$.
46. A fully mature embryo from a ripe seed. Root-cap is shown in black and plerome in dotted lines, *p* is the plumule. $\times 50$.
47. A few endosperm cells with prominent nuclei and starch-grains in the cytoplasm. $\times 600$.

TEXT-FIGURE E (p. 63).

48. Ovule before fertilization. The dotted area in figs. 48, 49, 50, 51, 52, and 53 represents the nucellar tissue surrounding the embryo-sac. $\times 100$.
49. Ovule immediately after fertilization showing the beginning of the campylotropous curvature. The embryo-sac has enlarged and the origin of the aqueous tissue as a micropylar cap is also represented. $\times 100$.
50. Ovule having attained the campylotropous form. The funicle is fused with the micropylar end. The oospore has divided once, and a number of free endosperm nuclei are distributed in the embryo-sac. $\times 100$.
51. Embryo at octant stage showing the further enlargement of the sac and the persistence of the nucellar tissue. $\times 30$.
52. The stage of cellular endosperm when the sac has reached its maximum size. The nucellus is still persistent. The embryo has now reached the lobing-of-the-cotyledons-stage. $\times 30$.
53. The mature seed with the perisperm (dotted) surrounding the embryo. $\times 50$.
54. Micropylar portion of the ovule showing funicular strands fused with the outer integument. *s*, sclerotic cells, *a*, aqueous tissue cells (both being specialized structures of the inner integument) merging into one another; *t*, tracheal tissue. The endosperm nuclei are in a state of simultaneous division. $\times 120$.

A revision of the British species of the genus *Agrostis* Linn. By W. R. PHILIPSON, B.A. (Communicated by Sir ARTHUR W. HILL, K.C.M.G., F.R.S., F.L.S.)

(With Plates 4-21, and with 40 figures and 9 graphs in the text)

[Read 28 October 1937]

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INTRODUCTION.

In an old-established genus with such a wealth of forms as *Agrostis* it is difficult to reconcile modern taxonomy with old nomenclature. This difficulty is at once encountered when the definition and limitation of the genus are attempted. The concept of the genus has changed since the time of Linnaeus, but it is desirable that the standard species should be as representative of Linnaeus's concept as is compatible with the modern limitations of the genus. With the increased knowledge of the floras of the world many new species have been included in *Agrostis*, and in many cases the conception of the genus has had to be broadened to include them. The result is that while there is a large nucleus of closely allied species, there are also numerous species which can be included only doubtfully in the genus, and this in turn results in the limitations of the genus being very vague and often a matter of convenience. The generic description given below (p. 76), while based on that of Stapf in Dyer, 'Flora Capensis', VII, p. 545, was drawn up after an examination of the species represented in the Kew Herbarium. It is not intended to include all the doubtful species, whose retention in, or exclusion from, the genus must be the subject of further research; it is intended to include only those species which undoubtedly belong to the genus.

The closely allied genera, *Calamagrostis* (with *Deyeuxia*), *Polypogon*, and *Apera*, were also examined ; and it soon became evident that no satisfactory distinction between these and *Agrostis* exists, so that their separation will have to be by arbitrarily chosen characters. Moreover, the tribe Agrostidae, as it is now understood, is by no means a natural group of genera, and it is to be hoped that in the future some character other than the single floret in the spikelet will be employed to define it.

The British species of *Agrostis* fall into two sections, *Trichodium* and *Vilfa*. This division of the genus is retained because of the very great number of species throughout the world in which the palea is minute. These species seem to form an alliance in contradistinction to those species with a longer palea.

In the construction of the Key, characters have been chosen which are truly diagnostic of the groups they are used to separate, and which, while readily observable, are free from differences of interpretation. For example, the length of the anthers is used to separate *A. stolonifera* and *A. semiverticillata*, because the roughness of the glumes and the density of the panicle cannot be precisely defined, and because the difference in size of the anthers can be detected without even the aid of a hand lens.

The treatment of each species follows a uniform plan. A description is given which is intended to include all the variations which are found within the limits of the species. When the species includes varieties, the group which is considered typical of the species is also treated as a variety, so that the species is subdivided into two or more groups of equal rank. Under the heading of minor variations are recorded such of the numerous variations and fluctuations as have received names in the past. In this way it is hoped that all the names which have been applied to British phenotypes of *Agrostis* and those based on exotic types which are applicable to British plants have been collected together, even though names are not applied to the variations in the present revision. An explanation of the status of the various categories into which the species have been divided is given in the section on 'Variation, fluctuation, and fixity of characters' (p. 105 forward).

The notes on the general distribution of the species throughout the world have been compiled from floras, and their records have not, for the most part, been checked by specimens ; but the distribution in the British Isles has been most rigorously checked. The figures chosen for citation are (i) those which best represent the plants, (ii) those of historic importance, and (iii) those in readily accessible works. Representative specimens of all the species and varieties, and of many of the smaller variations, are cited and are arranged according to the herbaria in which they occur, so that students may readily discover where they may most conveniently find specimens of each group. The herbaria are indicated by letters in Clarendon type as follows :—**K**. The Royal Botanic Gardens, Kew ; **B**. The British Museum Herbarium ; **W**. The National Museum of Wales, Cardiff ; **E**. The Royal Botanic Garden, Edinburgh ; **D**. The Druce Herbarium, Yardley Lodge, Oxford ; **C**. The Botany School, Cambridge.

The synonymy has been made as complete as possible. When a name has been wrongly applied, the name and original author are cited in inverted commas followed by the later author's name, e.g. when Withering applied *Agrostis alpina* Scop. to *A. setacea* Curt. the citation is given as '*A. alpina* Scop.' With. By this means incorrect identifications are distinguished from later homonyms.

In the second section variations and fluctuations are examined critically as they occur in the species and in populations. By such studies the true significance of the subdivisions of the species may be arrived at. The importance of recognizing the very great number of variations that can be found in an apparently uniform population cannot be too greatly stressed. These variations may be selected by the environment and, when the resultant ecological groups are sufficiently distinct, as they are in *A. stolonifera* var. *stolonifera*, they may be described as ecads—groups brought about and preserved by the environment.

The anatomy of the vegetative parts of the different species and varieties was investigated to determine their value as aids to identification. The anatomy is described in the third section, and the conclusion is reached that it is of very little use in the diagnosis of the species. Even the anatomy of the leaf-blade, which was very fully investigated, is essentially the same in all the species.

Complete life-histories are described (p. 134 forward), so that the characters, from germination to maturity, may become familiar, and none of consequence escape notice.

TAXONOMY.

The standard species.

The original description of the genus *Agrostis* appeared in Linnaeus's *Genera Plantarum*, ed. i, p. 19 (1737), and though he widened the scope of the genus when he published the first edition of his *Species Plantarum* (1753) by including unawned forms, he retained the original description in the 5th edition of the *Genera Plantarum*, which was published in the following year. It ran: 'Cal. *Gluma*, uniflora, bivalvis, acuminata. Cor. bivalvis, acuminata, vix longitudine calycis; altera majore aristata.'

The twelve species published in the *Species Plantarum* are divided into the sections *Aristatae* and *Muticae*; and the standard species of the genus should be among the former, since the description of the genus includes reference to an awn. It cannot be among the several Linnaean species removed to other genera by later authors, e.g. the first three and the last of the *Aristatae*, and the last three of the *Muticae*. Two aristate species are left, viz. *A. rubra* and *A. canina*; and since the identity of the former is uncertain (Hitchcock, Bot. Gaz. XXXVIII, p. 141, 1904), it seems best to select *A. canina* as the standard species of the genus *Agrostis*.

There are species, now generally considered to belong to the genus *Agrostis*, which have been removed by various authors and placed in new genera. Thus Adanson (1763) based a new genus—*Vilfa*—on Bauhin's *Gramen caninum*

supinum, which is quoted in synonymy under *A. stolonifera* by Linnaeus, while he retained the name *Agrostis* in the section *Avenae*, a group of genera which he describes as having a dorsal awn. At the same time in his index (p. 514) he quoted ' Scheuchzer 57 ' as a species of *Agrostis*; but this grass, which Scheuchzer figures (Tab. II, 4 A), probably belongs to the modern genus *Imperata*; and as it is unawned it must be considered to have been wrongly included by Adanson in his genus *Agrostis*. Michaux (1803) founded the genus *Trichodium* to include certain North American species in which the palea is minute and the lemma usually awnless. Schrader (1806) rightly included in Michaux's genus European species with a minute palea, whether unawned or awned; but Beauvois (1812) founded the genus *Agraulus* to include the awned species, retaining *Trichodium* only for those species with a minute palea and no awn. The size of the palea does seem to be of sectional importance in the genus; but the presence or absence of the awn should not be used as a generic or even a sectional character, as it is rarely either constantly present or constantly absent in any one species.

If these smaller genera should be revived, their correct nomenclature would depend on our conception of the typical *Agrostis*. If, for instance, we follow Hitchcock (' Genera of Grasses of the United States ', U.S. Dep. Agric. Bull. 772, p. 125; 1920) and select *A. stolonifera* as the standard species of the genus as now understood, the name *Vilfa* Adans. becomes a synonym of *Agrostis*, and the name *Trichodium* Michx. can be used for the species with minute paleae. On the other hand, if, as suggested above, *A. canina* be selected as the standard species, the name *Agrostis* is retained for the genus including *A. canina*; and *Vilfa* Adans. may be used as the correct name of a genus including *A. stolonifera*.

Maintaining that Adanson was correct in retaining the name *Agrostis* for the awned species, and in coining a new generic name for the unawned species when he decided to remove these to another genus, the standard species of *Agrostis* should not be selected from among the species included in Adanson's new genus; but from among the *Aristatae* of Linnaeus, and for reasons given above *A. canina* is the most suitable species.

Generic description.—Spikelets small, 1-flowered, hermaphrodite, in diffuse or dense panicles; rhachilla usually not continued beyond the floret, rarely produced as a point or bristle. *Glumes* equal or subequal, usually lanceolate and acute, rarely obtuse, and very rarely acuminate or awned, usually 1-nerved, keeled, scabrous on the keel and sometimes over the whole surface. *Lemma* shorter than or rarely equal to the glumes, broadly ovate, usually truncate, membranaceous, sometimes scabrid or tomentose, 5- or, less frequently, 3-nerved, the lateral nerves sometimes excurrent, awned from the back or awnless; callus glabrous or with minute tufts of hairs. *Palea* usually shorter than the lemma, sometimes very short or obsolete, hyaline, 2-nerved or nerveless. *Lodicules* 2, lanceolate, hyaline. *Stamens* 3. *Ovary* glabrous; styles distinct, short; stigmas plumose, laterally exserted. *Caryopsis* free, enclosed in the scarcely altered floret, oblong, more or less dorsally compressed, grooved in

front, rarely subterete ; embryo small ; hilum punctiform or elongate, usually basal.

Annual or perennial grasses, caespitose or widely creeping above or below the soil, the culms low or tall, erect or geniculate, the leaf-blades flat or involute, the ligule membranous. The panicles often delicately branched, open or contracted, sometimes spike-like ; spikelets numerous ; the glumes opening widely during flowering.

KEY TO THE BRITISH SPECIES AND VARIETIES OF AGROSTIS.

Palea less than $\frac{1}{2}$ the length of the lemma ; ligules of culm-leaves acute (*Sect. TRICHODIUM*).

- Radical leaves with a single ventral groove ; glumes rough *A. setacea*.
- Radical leaves with four or more ventral grooves ; glumes smooth *A. canina*.
- Rhizomes absent ; stolons present *A. canina var. fascicularis*.
- Rhizomes with scale-leaves present *A. canina var. arida*.

Palea more than $\frac{1}{2}$ the length of the lemma ; ligules of the culm-leaves obtuse (*Sect. VILFA*).

- Palea $\frac{1}{2}$ the length of the lemma or less ; anthers over 1 mm. long ; glumes persistent.
- Rhizomes with scale-leaves present ; panicle open in fruit.
- Ligule of sterile shoots shorter than broad *A. tenuis*.
- Rhizomes short ; plants tall or low *A. tenuis var. hispida*.
- Rhizomes long ; plants low (1 dm.) *A. tenuis var. humilis*.
- Ligule of sterile shoots as long as broad. *A. gigantea*.
- Culms prostrate below *A. gigantea var. ramosa*.
- Culms erect or geniculate *A. gigantea var. dispar*.
- Rhizomes absent ; panicle closing in fruit *A. stolonifera*.
- Innovations numerous, plants tufted at the centre ; blades about 5 cm. or less *A. stolonifera var. stolonifera*.
- Innovations few, plants not tufted ; blades longer than 5 cm. *A. stolonifera var. palustris*
- Palea and lemma subequal ; anthers less than 0.75 mm. long ; spikelets falling as a whole *A. semiverticillata*.

THE DESCRIPTIONS OF THE SPECIES AND VARIETIES.

SECTION I. TRICHODIUM (*Michx.*) *Trin.* Agrost. p. 112 (1820) *.

Species with the palea less than $\frac{1}{2}$ the length of the lemma.

Synonymy.—*Agrostis* Adans. Fam. des Plant. II, p. 32 (1763) : Bast. Fl. Maine et Loire, p. 27 (1809) : Beauv. Agrost. p. 21 (1812). *Trichodium* Michx. Fl. Bor.-Amer. I, p. 41 (1803) : Schrad. Fl. Germ. I, p. 198 (1806) : Beauv.

* The genera *Trichodium* Michx. (1803) and *Agraulus* Beauv. (1812) resemble each other in that both have a minute palea, but an awn is present in the latter and absent in the former. Trinius reduced them to sections of *Agrostis* without changing their sense in any way. The two sections are now united, and the epithet *Trichodium* is chosen in preference to *Agraulus* because it is based on the earlier generic name, and because it was the first to be used (as a generic name) in the present comprehensive sense by Schrader (1806).

op. cit. p. 5 (1812) : Roem. & Schult. Syst. Veg. II, p. 276 (1817) : Link, Enum. Hort. Berol. I, p. 69 (1821). *Agraulus* Beauv. op. cit. p. 5 (1812) : S. F. Gray, Arr. Brit. Plant. II, p. 149 (1821). *Agrostis*, sect. *Agraulus* (Beauv.) Trin. Agrost. p. 112 (1820) : Spreng. Syst. Veg. I, p. 178 (1825). *A.* sect. *Trichodium* (Michx.) Spreng. op. cit. p. 259 (1825) : Gaudin, Fl. Helv. I, p. 178 (1828) : Godr. in Gren. & Godr. Fl. Fr. III, p. 483 (1856) : Griseb. in Ledeb. Fl. Ross. VI, p. 439 (1853) : Schur in Oest. Bot. Zeit. IX, p. 50 (1859). *A.* sect. *Agrostio-typus* in part (spp. 5-9) Aschers. & Graebn. Syn. Mittel-europ. Fl. II, p. 171 (1899). *A.* sect. *Nardagrostis* Aschers. & Graebn. loc. cit. (1899). *A.* subgen. *Trichodium* sect. *Eutrichodium* Rouy, Fl. Fr. XIV, p. 65 (1913).

1. AGROSTIS SETACEA Curtis, General Obs. 4 (1787).

Diagnosis.—Palea minute ; lemma 5-nerved, awned ; glumes uniformly scabrid ; panicle closed in fruit ; radical leaf with its blade setaceous, and its ligule acute ; caespitose. Anthers 1.5-2 mm. long.

Description.—A densely caespitose perennial, growing in isolated tufts or forming a close turf. Culms 2-6 dm. high erect, sometimes slightly geniculate below, rough, especially above, pale greyish green, usually with three brown nodes. Sterile shoots numerous at the base, intravaginal, never elongating as stolons. Leaf-sheath open above, closed below, terete, striated, slightly rough, rather loose, tapering towards the ligule, those of the culm-leaves green, of the radical leaves straw-coloured, the sheath of the lowest node of the culm longer than the internode, of the uppermost considerably shorter. Ligule up to 4 mm. long, acute, membranaceous, often torn. Blade of the sterile shoots up to 20 cm., usually shorter, filiform, about 0.3 mm. broad, with a slightly wider insertion and tapering gradually to the apex, elliptical in section, with a groove on the upper side, rough, pale or dark greyish green, rather stiff and erect, the blades of the culm-leaves 5 cm. or less, as the radical leaves or with two or four ventral grooves. Panicle 3-10 cm. long, spike-like before and after flowering, open to a varying extent during flowering ; rhachis straight, rough, green or purple, lowest internode longest, 0.8-1.5 cm. ; branches semi-verticillate, the lower up to 4 cm. long, minutely rough, the longer branches naked for half their length, the shorter with spikelets to the base ; branchlets in groups of two or three, minutely rough ; pedicels variable in length, up to 4 mm. Spikelets lanceolate when closed. Glumes 3-4 mm. long, the lower slightly longer, lanceolate, with an acute apex, tinged with pale or deep purple, toothed on the upper $\frac{2}{3}$ or $\frac{1}{2}$ of the keel and slightly on the margin, and covered with a fine uniform asperulence ; rhachilla short ; callus with two tufts of hairs, 0.5 mm. long. Lemma $\frac{2}{3}$ the length of the glumes, broadly ovate when flattened, truncate, with a minute scaberulence except at the apex, 5-nerved, the two marginal nerves shortly excurrent, the median nerve entering an awn near the base of the lemma ; the awn usually projecting considerably beyond the glumes, usually bent near the middle, twisted below. Palea very minute, shorter than the rhachilla hairs, bifid. Lodicules about 0.4 mm. long. Anthers

1·5–2·0 mm., sometimes tinged with purple. *Ovary* ovoid, less than 0·5 mm. long. *Caryopsis* about 1·5×0·4 mm.

Type.—No authentic specimens of Curtis have been preserved. There is a specimen in the British Museum Herbarium, originally from Curtis's garden, which may be taken as representative of the species.

*Synonymy**.—*A. canina* var. γ Huds. Fl. Angl. ed. 2, I, p. 31 (1778) †. '*A. alpina* Scop.' With. Bot. Arr. ed. 2, I, p. 71 (1787). '*A. filiformis* Vill.' Bast. Fl. Maine et Loire, p. 28 (1809). *Vilfa setacea* (Curtis) Beauv. Agrost. p. 182 (1812) ‡. *Trichodium setaceum* (Curtis) Roem. & Schult. Syst. Veg. II, p. 280 (1817). *Agraulus setaceus* (Curtis) S. F. Gray, Arr. Brit. Pl. II, p. 149 (1821).

With the spikelets not tinged with purple—*A. setacea* var. *flavida* Rouy, Fl. France, XIV, p. 70 (1913); deeply tinged with purple—*Agraulus setaceus* var. *purpureus* S. F. Gray, Brit. Pl. II, p. 150 (1821). A form with two flowers in the spikelets—*Agrostis setacea* var. *biflora* Lange in Willk. & Lange, Fl. Hisp. I, p. 54 (1861)—recorded from Spain.

Figures.—Curtis, Fl. Lond. VI (date ?), pl. 12: Sowerby & Smith, Eng. Bot. XVII (1803), pl. 1188: Parnell, Grass. Brit. II (1845), pl. 83.

Representative specimens.—K. S. DEVON: Haldon, Borrer. N. DEVON: Cawsand, Sherrin. E. SUSSEX: Heathfield, Borrer (in Borrer Herb.). SURREY: Lightwater, Turrill. B. N. DEVON: between Ashbury and Beaworthy, Rogers. SOMERSET: Cathelston, Marshall. SURREY: Camberley, Beeby. GLAMORGAN: St. Donats, Riddelsdell. W. GLAMORGAN: Mynydd-y-Glen, Wade; Pontyrhyl, Webb. W. SUSSEX: St. John's Common, Bailey. E. CORNWALL: Ponsanooth, Hamilton Davey. D. S. HANTS: Bournemouth, Linton. C. DORSET: Wareham, White. 167 sheets have been examined.

Distribution.—South-west Europe, in Spain, Portugal, W. France (not in Holland, see Prod. Fl. Bat. ed. 3, p. 2193; 1916). British Isles: dry sandy

* *A. setifolia* Brot. Fl. Lusit. I, p. 74 (1804) is a nomenclatural synonym for *A. alpina* Scop., Fl. Carniol. I, p. 60 (1772).

† The name *Agrostis setacea* was first published with a description by Curtis in the *Flora Londinensis* in 179—(the exact date is uncertain; see Clarke in Journ. Bot. XXXIII, p. 112, 1895), but in August 1787 it was included by Curtis in a list of British grasses with the citation 'H. [Hudson] var. *canina* γ '. The description in the *Flora Londinensis* is antedated by *A. setacea* Vill. (Hist. Dauph. II, p. 76; 1787), but this name was probably published later than August (since it is not mentioned in the *Göttingische Anzeiger* until 17 January 1788). The validity of the name *A. setacea* Curtis therefore rests on the identity of Hudson's variety. The identification of this variety with Curtis's plant is upheld by Hudson's slight description: 'foliis setaceis rigidis glaucis, culmo erecto', and by the locality given by Hudson: 'in ericetis montosis aridis, supra Hall Down prope Exeter et alibi in Devonia'. There is now no Hall Down near Exeter, but this locality is almost certainly the Haldon, where Borrer collected *A. setacea*. If Hudson's statement that his variety changes in moist soil into the typical *A. canina* is an error (as I think it may be, as he also states that the caespitose *A. canina* changes into the stoloniferous variety), then his var. γ is most likely to be *A. setacea* Curtis, which therefore can be retained as the correct name for this species.

‡ Beauvois cites Poiret, who makes *A. setacea* Curtis a doubtful variety of *A. rupestris* All.

and peaty heaths and chalk downs in the south and south-west. Ascending to 1,400 ft. (430 m.) in Somerset. Recorded from vice-counties 1-5, 8-14, 17, 22.

Flowering period.—From mid-June to July.

2. *AGROSTIS CANINA* Linn. Sp. Pl. ed. 1, 1, p. 62 (1753).

Diagnosis.—*Palea minute*; *lemma 5-nerved, usually awned*; *glumes smooth*; *panicle closed in fruit*; *radical leaf with its blade linear, and its ligule acute*; *caespitose or with overground stolons*. Anthers 1-1.5 mm.

Description.—A perennial of diverse habit. Caespitose or forming a turf with usually short rhizomes, or with often very long trailing sterile stolons. Culms from 1-6 or rarely 8 dm., usually about 4 dm. long, erect or geniculate, sometimes decumbent and rooting at the lower nodes, green or tinged with purple, sometimes rough above, with 4-6 brown or purple nodes. Sterile intravaginal shoots numerous, either all short and tufted, with the blades close together and hardly spreading, or some elongating as stolons, also extravaginal shoots with scale-leaves may be present. Leaf-sheaths split almost to the base, terete, striate, smooth, close-fitting, green or tinged with purple, especially near the ligule and the node, the sheaths of the lower nodes of the culm longer than the internodes, of the upper much shorter. Ligule up to 3 mm. long, usually much shorter in the leaves of the sterile shoots, acute, membranaceous, often torn. Blade up to 2 dm. long, the upper blades of the culm often very short, 1-3 mm. broad, folded or rolled in the bud, tapering gradually from the base to a filiform apex, pale to dark green or often greyish green, frequently rough, the upper surface strongly furrowed, flat or involute. Panicle 4-15 cm. long, in flowering ovoid or pyramidal, diffuse, in fruiting the branchlets are contracted against the branches, and these are raised more or less, especially the upper, producing a spike-like appearance; rhachis straight or angled only at the uppermost nodes, quite smooth below, rarely throughout, green or purple, first or second internode the longest, 1-1.8 cm. long; branches triangular with minute scabridity on the angles, especially above, rarely entirely smooth, dividing at about half their length; branchlets usually in unequal pairs, rarely quite smooth; pedicels very rarely smooth. Spikelets lanceolate. Glumes 1.5-4 mm. long, the lower slightly the longer, broadly to narrowly lanceolate with acute apices, pale green, very rarely yellowish when in flower, more usually tinged, sometimes very deeply, with purple, the margins colourless and shining, sometimes denticulate near the apex, the keel of the lower glume toothed on the upper $\frac{2}{3}$ or $\frac{1}{2}$, the upper glume with fewer teeth or none; the hairs of the callus very short. Lemma $\frac{2}{3}$ the length of the glumes, ovate when flattened, truncate, with a close asperulence except towards the apex, 5-nerved, the lateral nerves usually slightly excurrent, the median nerve usually entering an awn below the middle of the lemma, or ending blindly between the middle and the apex, the awn frequently twice the length of the lemma and bent, or shorter and straight, or entirely absent. Palea very minute, usually much shorter than the ovary, bifid. Lodicules about 0.4 mm. long. Anthers 1-1.5 mm.

long, frequently tinged with purple. *Ovary* ovoid, about 0·5 mm. long. *Caryopsis* about 1·1 × 0·3 mm.

Type.—*Agrostis* sheet No. 12 in the Linnaean Herbarium *.

Distribution.—Throughout Europe, and Asia from the Caucasus and Himalayas northwards. Introduced into N. America (? native in Newfoundland); closely related forms in New Zealand, Patagonia, and the Falklands. Throughout the British Isles; Channel Isles.

Flowering period.—From mid-June to July.

Var. FASCICULARIS (*Curtis*) *Sinclair*, *Hort. Gram. Wob.* p. 278 (1824).

The *culms* frequently decumbent, rooting and branching freely at the lower nodes. The intravaginal *branches* frequently elongated as stolons, which are often long and rooted at most of the nodes, where clusters of short extravaginal branches arise. When growing in very wet situations the habit is very lax, with long trailing stolons and large panicles. The *leaves* are usually narrow, pale green, and soft. The branches of the *panicle* frequently become only slightly raised against the rhachis after flowering. *Spikelets* 2–4 mm. long. *Lemma* with or without an awn of variable length. Growing usually in damp situations, sometimes floating in ditches.

Type.—The specimen in Sinclair's own copy of the folio edition of *Hortus Gramineus Woburnensis*, which is preserved at Woburn Abbey, may be taken as the type of this variety.

Synonymy.—*A. canina* Linn. Sp. Pl. ed. 1, i, p. 62 (1753); With. Bot. Arr. ed. 1, p. 30 (1762); Roth, Tent. Fl. Germ. i, p. 31 (1788); Sibth. Fl. Oxon. p. 36 (1794); Smith, Fl. Brit. ed. 1, i, p. 78 (1800); Host, Fl. Austr. i, p. 99 (1827); Bab. Man. Brit. Bot. ed. 1, p. 360 (1843). *A. canina* var. α Huds. Fl. Angl. ed. 2, i, p. 30 (1778). *A. tenuifolia* Curtis, General Obs. p. 4 (1787). *A. mutabilis* Sibth. op. cit. p. 36 (1794) †. ‘*A. vinealis* Schreb.’ With. op. cit. ed. 3, ii, p. 127 (1796) ‡. *A. fascicularis* Curtis, Practical Obs. ed. 3, p. 46 (1800), nomen; Sinclair, *Hort. Gram. Wob.* ed. 1, p. 154 (1816). *Trichodium caninum* (Linn.) Schrad. Fl. Germ. i, p. 198 (1806). *Agrostis hybrida* Gaudin, Agrost. Helv. p. 66 (1811) §. *Agraulus caninus* (Linn.) S. F. Gray, Brit. Plant. ii, p. 148

* The specimens consist of panicles and part of the culms only, so that it is impossible to determine to which variety they belong. There are three other specimens pinned to this sheet (which implies that Linnaeus considered them probably the same species), and as the first of these is *A. canina* var. *fascicularis*, and as the other two specimens belong to *A. stolonifera* Linn., it is clear that Linnaeus had a stoloniferous plant in mind. The diagnosis in the *Species Plantarum* is insufficient, but the citations of Bauhin and Scheuchzer, and the habitat, all support the view that Linnaeus had the stoloniferous variety in mind.

† This species is included in his sect. *Muticae*, but he refers to Scheuchzer (Agrost. taf. 3, fig. 9 c), which is of an awned species.

‡ The palea is described as nearly equal to the lemma. This is probably an error, or Withering may have been describing an awned form of *A. stolonifera* Linn. Gaudin (Agrost. p. 87; 1811) suspects that *A. vinealis* Schreb. is an awned form of *A. decumbens*.

§ A specimen collected by Gay in the company of Gaudin ‘au bord du Katzensee (lacus felinus)’ in 1805 is in the Kew Herbarium.

(1821). *Agrostis canina* var. *hybrida* (Gaud.) Gaudin, Fl. Helv. I, p. 182 (1828). *A. canina* var. *genuina* Godr. in Gren. & Godr. Fl. Fr. III, p. 484 (1856). *A. canina* var. *stolonifera* Blytt, Norg. Fl. I, p. 81 (1861).

Figure.—Hoffmann, Deutschl. Fl. I, pl. 6 (1800).

Representative specimens.—**K. SURREY**: Wimbledon Common, *Turrill*; Richmond Park, *Philipson* 167; Black Pond, Oxshott, *Hubbard*. **CARDIGAN**: Borth Bog, *Philipson* 156. **NORTHUMBERLAND**: *Philipson* 202-4. **B. E. CORNWALL**: between Polscove and Polbathick, *Briggs*. **SURREY**: Esher, *Britton* 703. **CARDIGAN**: Pont-ar-fynach, *Augustine Ley*. **CUMBERLAND**: Cross Fell, *Baker*. **W.** No locality: *Conway* in 1834. **E. DUMFRIES**: Bruce's Castle, *Webb*. **D. BERKSHIRE**: Wellington College, *Druce*. **CAMBRIDGESHIRE**: Wimblington, *Fryer*. **LINCOLNSHIRE**: Bourne, *Webster*. **C. CAMBRIDGESHIRE**: March, *Fryer*. 125 sheets have been examined.

Distribution.—Probably throughout the British Isles in low-lying grassland, but imperfectly known.

Var. *ARIDA* Schlechtendal, Fl. Berol. I, p. 45 (1823).

Differing from the preceding mainly in habit. Caespitose or spreading underground to form a turf. Culms erect or geniculate, infrequently rooting at the lower nodes, and branching sparingly. The intravaginal branches not elongating as stolons; extravaginal branches with scale-leaves are present, either at once ascending, or spreading, often widely, as rhizomes with narrow, straw-coloured scale-leaves, and occasionally with solitary branches at few of the nodes, and producing at the surface a tuft of intravaginal branches. The panicle usually becomes spike-like after flowering. Spikelets 2-4 mm. long. Lemma with or without an awn of variable length. Growing on heaths and acid grassland.

Type.—No specimen has been preserved.

Synonymy.—*A. canina* var. β Huds. Fl. Angl. ed. 2, I, p. 30 (1778). *A. stricta* Curtis, Obs. Brit. Grass. ed. 4, p. 35 (1804): Sinclair, Hort. Gram. Wob. ed. 1, 150 (1816). *A. capillaris* Sinclair, op. cit. 182 (1816). ‘*A. canina* Linn.’ Hook.* Fl. Scot. p. 24 (1821): Blytt, Norg. Fl. I, p. 80 (1861): Rouy, Fl. Fr. XIV, p. 66 (1913). *A. canina* var. *sylvatica* † Schlechtend. Fl. Berol. I, p. 45 (1823). *A. canina* var. *capillaris* Sinclair, op. cit. ed. 2, p. 300 (1824). *A. canina* var. *vulgata* Döll, Rhein. Fl. p. 108 (1843). ‘*A. canina* var. *genuina* Godr.’ Aschers. & Graebn. Syn. Mittel-europ. Fl. II, p. 184 (1899).

Figures.—Host, Ic. Gram. Aust. IV (1809), pl. 53: Reichenbach, Agrost. Germ. (1834), pl. 33, fig. 1424: Parnell, Grass. Scotl. (1842), pl. 15.

* This variety of *A. canina* has latterly become to be regarded as the typical form of the species. In England this interpretation probably began with Hooker, who would find the caespitose variety much the more numerous in Scotland; he includes stoloniferous plants in his description.

† The varietal epithet *arida* is selected in preference to *sylvatica* because of the inappropriateness of the latter.

Representative specimens.—**K.** SOMERSET: Porlock, *Maynard*. SURREY: Richmond Park, *Hubbard* in 1928. NORFOLK: Dersingham, *Hubbard* 9273. CARDIGAN: Pwell Peiran, *Philipson* 179. NORTHUMBERLAND: Sweethope, *Philipson* 194. **B.** SURREY: Wimbledon, *Moore*. KENT: Forest Hill, *Sowerby*. ESSEX: Walthamstow, *Forster*. ISLE OF MAN: Grindle, *Holt*. **W.** GLAMORGAN: Caerphilly Common, *Wade* and *Hyde* in 1931. **E.** ORKNEY: Kirkbister, *Johnston* 837. **D.** LEICESTER: Peckleton Common, *Horwood*. **C.** CAMBRIDGESHIRE: Horse Moor, Wimblington, *Tutin* and *Gilmour*. 412 sheets have been examined.

Distribution.—Throughout the British Isles; abundant on heaths and upland grass.

Minor variations.

1. The awn absent, or short and straight, the median nerve ending about the middle of the lemma or rarely continued to the apex. Otherwise as in the awned form and with the same distribution.—*A. canina* var. *mutica* Gaud. Fl. Helv. i, p. 182 (1828). *A. canina* var. *pudica* Döll, Rhein. Fl. p. 108 (1843). *A. canina* var. *submutica* Čelak. Fl. Böhm. iv, p. 710 (1881).

Representative specimens.—**K.** WESTMORLAND: Patterdale, *Philipson* 197. **B.** WARWICKSHIRE: Balsall Common, *Bromwich* 1655. **FIFE:** Balmuto, *Syme*. **D.** CHESHIRE: Oakmere, *Holt*.

2. Spikelets large, with glumes 3–4 mm. long. Radical leaves often broad and flat. Moorland in the west and north, especially in the Highlands.—*A. vinealis* Schreb. Spicil. Fl. Lipsic. p. 47 (1771): With. Bot. Arr. ed. 2, i, p. 72 (1787). *A. canina* var. *elatior* Hartm. Scand. Fl. ed. 2, p. 19 (1832). ‘*A. canina* var. *hybrida* Gaud.’ Schur in Oestr. Bot. Zeitschr. ix, p. 52 (1859). *A. canina* var. *grandispiculata* Schur, loc. cit. (1859). *A. canina* var. *scotica* Hack. ex Druce in Bot. Exchange Club Rep. for 1889, p. 274 (1890)*. *A. canina* var. *grandiflora* Hack. ex Druce in Scot. Nat. x, p. 293 (1890). *A. canina* var. *laevis* Hack. ex Druce in Irish Nat. xvi, p. 152 (1907).

Representative specimens.—**K.** MIDLOTHIAN: Pentlands, *Balfour*. PERTH: Ben Lawers, *Don*. **B.** WESTMORLAND: Fairfield, *Ridley*. PERTH: Ben Lawers, *Robert Brown* in 1794 as ? *A. vinealis* Schreber’. ABERDEENSHIRE: between Clova and Invercauld, *Robert Brown* in 1794 named ‘var. *montana*’. W. ROSS: Ben Eay, *Druce* (var. *scotica* Hack.). KERRY: Brandon Mts., *Druce* (var. *laevis* Hack.). **D.** ABERDEENSHIRE: Glen Callater, *Druce*, with the name f. *coarctata*. W. ROSS: Ben Eay, *Druce* (var. *scotica* Hack. and var. *grandiflora* Hack.). KERRY: Brandon Mts., *Druce* (var. *laevis* Hack.).

* This grass does not approach *A. rupestris* All. as suggested by Druce. *A. canina* and *A. rupestris* are distinct species, most readily and surely separated by the smaller anthers in the latter.

3. The glumes deeply tinged with purple.

Representative specimen.—D. PERTH: Lochan Larig, *Druce*, with the sub-varietal name *nigrescens*.

4. Plants low, culms rarely over 15 cm. The dwarf habit is retained on cultivation. Growing on high mountains.—? *A. pusilla* Dumort. Obs. Gram. Belg. p. 129 (1823). *A. canina* var. *alpina* Parnell, Grass. Scot. p. 37 (1842). ? *A. canina* var. *humilis* Willk. in Willk. & Lange, Fl. Hisp. I, p. 54 (1861). ? *A. canina* var. *pusilla* (Dumort.) Aschers. & Graebn. Syn. Mittel-eur. Fl. II, p. 185 (1899).

Representative specimens.—K. CUMBERLAND: Dale Head, summit, *Philipson* 196. D. INVERNESS: Skye, *Druce* as f. *macra* Hack.

5. The glumes green, without any tinge of purple. A shade form which becomes darker when grown in open situations.—*A. pallida* * Hoffm. Deutsch. Fl. ed. I, I, p. 34 (1800). *A. canina* var. γ Hook. Fl. Scot. p. 24 (1821). *A. canina* var. *pallida* (Hoffm.) Rouy, Fl. Fr. XIV, p. 67 (1913).

Representative specimens.—K. CORNWALL: Perranzabuloe, *Rilstone*. B. GLAMORGAN: Pontneathvaughn, *Riddelsdell*. D. BERKSHIRE: Fence Wood, *Druce*. E. INVERNESS: Philmorach Falls, Beauly, *Druce*.

6. The glumes at all times pale yellow or yellowish green.—*A. nivea* (vel *Trichodium niveum*) Sinclair, Hort. Gram. Wob. folio 152 (1816). *A. canina* var. β Hook. Fl. Scot. p. 24 (1821). *A. canina* var. *varians* Aschers. & Graebn. Syn. Mittel-eur. Fl. II, p. 185 (1899) †.

Representative specimens.—K. SCOTLAND: without precise locality, *Don*. D. CHESHIRE: Fish Pool, *Holt*.

Diseased states.

1. Infection with *Anguillina agrostis* (Steinbuch) Goodey. Symptoms as in *A. tenuis* (see p. 89). Rare.

Representative specimen.—B. MIDDLESEX: Hampstead, *Buddle* (in Buddle's Herb.).

2. Infection with *Tilletia decipiens* (Pers.) Körn. Symptoms as in *A. tenuis*. Infrequent.

Representative specimens.—K. SHETLANDS: Foula, *Gladstone*. B. KENT: Tunbridge Wells, *Forster* (2 sheets).

* Hoffmann cites (with a note of doubt) *A. pallida* With. Bot. Arr. ed. 3, II, p. 128 (1796). The description of this latter grass would conform to this variation of *A. canina* but for having the 'inner valve deciduous, more like a very short slender hair than a husk, and so minute that it is with difficulty found'.

† Based on *A. varians* Thuill. (Fl. Par. ed. 2, p. 35; 1799), but this description mentions a reddish panicle. Rouy doubtfully gives *A. varians* Thuill. as a synonym for *A. canina* var. *mutica* Gaud.

SECTION 2. VILFA (*Adans.*) *Roem. & Schult.*

. Syst. Veg. II, p. 343 (1817).

Species with the palea more than $\frac{1}{2}$ the length of the lemma.

Synonymy.—*Vilfa* Adans. Fam. des Plant. II, p. 495 (1763) : Beauv. Agrost. p. 16 (1812) : S. F. Gray, Brit. Plant. II, p. 144 (1821). *Agrostis* Schrad. Fl. Germ. I, p. 207 (1806) ; S. F. Gray, loc. cit. (1821). *Decandolia* Bast. Fl. Maine et Loire, p. 28 (1809). *Agrostis* sect. *Agrostis* (Linn.) Trin. Agrost. p. 111 (1820) ; Gaudin, Fl. Helv. I, p. 185 (1828). *A.* sect. *Vilfa* (Adans.) Link, Enum. Hort. Berol. I, p. 70 (1821) : Spreng. Syst. Veg. I, p. 257 (1825). *A.* sect. *Euagrostis* Godr. in Gren. & Godr. Fl. Fr. III, p. 481 (1850) : Griseb. in Ledeb. Fl. Ross. IX, p. 463 (1853) : Schur in Oestr. Bot. Zeitschr. IX, p. 44 (1859). *A.* sect. *Agrostiotypus* in part (spp. 1-4) Aschers. & Graebn. Syn. Mittel-europ. Fl. II, p. 171 (1899). *A.* subgen. *Vilfoideae* and *Vilfa* Rouy, Fl. Fr. XIV, pp. 59 & 60 (1913).

3. AGROSTIS TENUIS *Sibthorp*, Fl. Oxon. p. 36 (1794).

Diagnosis.—Palea half the length of the lemma or longer ; lemma usually 3-nerved, occasionally awned ; glumes smooth ; panicle remaining open in fruit ; radical leaf with its blade linear and its ligule shorter than broad, blunt ; caespitose or stoloniferous. Anthers 1-1.5 mm.

Description.—A perennial which often forms a dense turf, caespitose, spreading by usually short rhizomes or, in addition, with short or occasionally long stolons. Culms usually from 2-5 dm., but varying from 2 cm.-10 dm. long, usually erect or geniculate, often procumbent and branching, finally becoming upright or inclined, sometimes remaining almost horizontal, green or tinged with purple, smooth or rarely rough below the panicle, with 3-5 yellow or brown nodes. Sterile shoots usually with blades distant and markedly distichous and spreading at an angle of 30-45°, the intravaginal shoots often becoming elongated as stolons, sometimes long and much branched, the extravaginal usually short with few brown scales, sometimes long with branches in the axils of the scale-leaves ; scale-leaves split at the apex. Leaf-sheaths open above, closed near the base, terete, striate, smooth, close fitting, green or occasionally tinged with purple, the sheaths of the lower nodes of the culm longer than the internodes, the upper usually shorter, occasionally longer. Ligule of the sterile shoots usually less than 0.75 mm., rarely up to 1 mm., of the upper culm-leaves often longer, truncate or very obtusely rounded, membranaceous. Blade up to 2.5 dm. long, the upper blades of the culm often very short, 1-5 mm. broad, parallel-sided or sometimes broadest above the base, rolled in the bud, pale to dark green, sometimes greyish or tinged with purple, slightly rough on both surfaces, furrowed above, flat or involute. Panicle 1-20 cm. long, erect or nodding above, in flowering ovoid, cylindrical or pyramidal, diffuse, rarely spike-like, the spikelets of adjacent verticils intermingling, in fruiting the branches and branchlets may remain spreading or the ultimate branchlets may become parallel,

forming bunches of spikelets, rhachis usually angled at the uppermost nodes, sometimes straight throughout, entirely smooth or slightly rough above, rarely throughout, green or tinged with purple, first or second internode longest, up to 3 cm. long, branches semi-verticillate, up to 10 cm. long, triangular, entirely smooth or with scabridity at the angles, especially above, rarely throughout, dividing at about half their length, usually angled at the nodes; branchlets usually in unequal pairs, smooth or minutely rough; pedicels smooth or rough. *Spikelets* lanceolate. *Glumes* 2-3.5 mm. long, the lower slightly the larger, broadly to narrowly lanceolate, with acute apices, pale green, at least on the midrib, or usually tinged with purple, especially between the keel and the margins which are usually colourless and shining, the keel of the lower glume usually slightly toothed in its upper half, of the upper glume usually smooth; the hairs of the callus short. *Lemma* $\frac{2}{3}$ the length of the glumes, broadly ovate when flattened, rounded at the apex, with a scattered asperulence towards the base, 3-nerved at least in the upper half, rarely 5-nerved, the two marginal nerves usually shortly excurrent, the median nerve usually ending just below the apex, sometimes excurrent between the apex and the middle of the back of the lemma as an awn which is usually short but may protrude considerably beyond the glumes. *Palea* $\frac{1}{2}$ - $\frac{2}{3}$ the length of the lemma, bifid, faintly 2-nerved. *Lodicules* about 0.4 mm. long. *Anthers* 1-1.5 mm. long, sometimes tinged with purple. *Ovary* ovoid, about 0.4 mm. long. *Caryopsis* about 1.0×0.35 mm.

Type.—There is a sheet in the Fielding Herbarium, Oxford, written up by Sibthorp as the *A. tenuis* of the *Flora Oxoniensis*. There are two specimens on the sheet: the one to the right is awned, but is without doubt *A. tenuis*; the other specimen being unawned, and therefore agreeing better with this description may be taken as representative of *A. tenuis* Sibth.

Distribution.—Throughout Europe, Northern Asia and N. America. Introduced into New Zealand, Australia, and Tasmania. Throughout the British Isles; Channel Isles.

Flowering period.—From late June to August; maximum early in July.

Var. HISPIDA (Willd.) Philipson, comb. nov.

Plants of diverse habit and stature. Densely or loosely caespitose, with or without stolons, which may be short or long and trailing. *Leaves* usually flat and lax, sometimes rolled and rigid. *Panicle* diffuse. *Lemma* 3-nerved, unawned or 5-nerved and awned. Heaths, moorland, and pastures, especially in hilly districts and on dry soil.

Type.—Willdenow's specimen is in the Herbarium of the Botanical Museum, Berlin.

Synonymy.—‘*A. capillaris*’ With. Bot. Arr. ed. 2, i, p. 73 (1787) *. *A. tenuis*

* *A. capillaris* Linn. (Sp. Pl. ed. 1, p. 62; 1753) is of uncertain application. Of the diagnosis the words ‘capillari, patente’ are original, ‘flosculis muticis’ are taken from Linnaeus's *Flora Suecica* (p. 23; 1745), and the remainder is copied from Royen's *Flora*

Sibth. Fl. Oxon. p. 36 (1794). *A. vulgaris* With. Bot. Arr. ed. 3, II, p. 132 (1796). *A. hispida* Willd. Sp. Pl. I, p. 370 (1798). *Decandolia vulgaris* (With.) Bast. Fl. Maine et Loire, p. 28 (1809). *Agrostis vulgaris* var. *hispida* (Willd.) Gaudin, Fl. Helv. I, p. 191 (1828); Schur in Oestr. Bot. Zeitschr. IX, p. 46 (1859). *Vilfa vulgaris* (With.) S. F. Gray, Brit. Pl. II, p. 146 (1821). *Agrostis vulgaris* var. *mutica* Sinclair, Hort. Gram. Wob. ed. 2, p. 269 (1824). *A. vulgaris* var. *plena* Meyer, Fl. Kön. Hanov. III, sig. 22* (1842). *A. vulgaris* var. *genuina* Schur in op. cit. p. 45 (1859). *A. alba* var. *vulgaris* (With.) Plues, Brit. Grass. p. 151 (1867); Thurb. ex S. Wats. Bot. Calif. II, p. 272 (1880). *A. polymorpha* var. *brevi-ligulata* Neirl. Fl. Wein, ed. 2, I, p. 26 (1868). *A. stolonifera* var. *vulgaris* (With.) Čelak. Fl. Böhmk. IV, p. 710 (1881). ' *A. stolonifera* Linn.' Farw. in Mich. Acad. Rep. for 1919, p. 350 (1920). *A. stolonifera* var. *hispida* (Willd.) Farw. in op. cit. p. 351 (1920). *A. alba* var. *tenuis* (Sibth.) Fiori, Fl. Anal. d'Ital. I, p. 97 (1923).

Figures.—Sowerby & Smith, Eng. Bot. xxiv, pl. 1671 (1807) : Host, Gram. Aust. IV, pl. 59 (1809); Sinclair, Hort. Gram. Wob. facing p. 269 (1824) : Parnell, Grass. Scot. pl. 12 (1842).

Representative specimens.—K. CHANNEL ISLES : Sark, Ballard 421. SURREY : Oxshott Heath, Philipson 119 ; Box Hill, Philipson 123 ; Richmond Park, Philipson 115. HERTFORDSHIRE : Hadley Wood, Hubbard G 56. NORFOLK :

Leydenensis (p. 59 ; 1740). After the habitat is appended a further, original, descriptive sentence : ' *Panicula vere capillaris, tenuissimisque pedicellis singularis*' . The diagnosis is evidently based on that of Royen, although emended and extended ; the reference to Dalibard is of little importance, as his diagnosis is taken direct from the *Flora Suecica* of Linnaeus. Royen's diagnosis, with the words ' *panicula compressa*' , is not applicable to *A. tenuis* Sibth., and his reference to Scheuchzer (Agrost. p. 129 ; 1719) is to a grass with a long, rather pointed ligule. Of the other authors cited by Royen, the description of Bauhin (Theatri Bot. ; 1658) is unidentifiable, that of Monti (Gram. p. 52 ; 1719) is based on Petiver (Conc. Gram. p. 120 ; 1716), as is that of Ray (Syn. p. 402 ; 1724), and these probably refer to *A. tenuis* Sibth. It seems certain that Linnaeus has taken Royen's diagnosis and, after emending it, applied it to another grass. The identification of this grass is uncertain, but it is most probably *A. tenuis* Sibth. There are two specimens in the Linnaean Herbarium written up as *Agrostis capillaris* by Linnaeus. The number of *A. capillaris* is underlined in his own copy of the *Species Plantarum* (ed. 1), which implies that a specimen was in the herbarium about 1753, and perhaps earlier. One specimen is *A. delicatula* Pourr., a plant of southern Spain. The other sheet was sent to Linnaeus by Seguier with a reference to his book—*Plantae Veronenses, Supplementum*—which was published in 1754. This specimen is *A. stolonifera* Linn. If there was a specimen named *A. capillaris* in the herbarium when the *Species Plantarum* was written it must have been the Spanish plant, which Linnaeus had confused with the Lapland plant. The name *A. capillaris* cannot be used for *A. delicatula* Pourr., and the confusion has been increased by the application of the name *A. capillaris* to four other distinct Spanish species. Nor can it be used for *A. tenuis* Sibth., as it is impossible to be certain that this was the plant Linnaeus had in mind, and because his diagnosis is largely taken from another author who was describing a different species. *A. capillaris* Huds. (1762) and *A. polymorpha* var. *capillaris* Huds. (1778) are identifications of a British plant with that of Linnaeus, and no original description is given.

Appleton, *Hubbard*, 9288. YORKSHIRE: Richmond, *Philipson* 105. WEST-MORLAND: Patterdale, *Philipson*, 107. NORTHUMBERLAND: Wolsington, *Philipson* 111. B. MIDDLESEX: Finchley Road, *Thiselton Dyer*. N. STAFFORD-SHIRE: between Trentham and Clayton, *Rendle*. CAERNARVON: Bardsey, *Butler*. W. YORKSHIRE: Ilkley, *Middleton* W. GLAMORGAN: Caerphilly, *Wade*. CARDIGAN: Devil's Bridge, *Wade*. CARMARTHEN: Llandovery, *Jones*. E. MIDLOTHIAN: Queensferry, *Greville*. D. DORSET: Studland Bay, *Palmer*. NORTHUMBERLAND: Otterburn, *Fox*. C. DERBYSHIRE: Matlock, *Spencer*. KENT: High Barns, *Miller*. HEREFORDSHIRE: Hitchin, *Little*. 760 sheets have been examined.

Distribution.—Throughout the British Isles.

Minor variations.

1. The lemma in some or all the spikelets 5-nerved, and the median nerve excurrent near the middle as a dorsal awn of variable length. Probably co-extensive in distribution with the unawned form.—*A. canina* With.* Bot. Arr. ed. 3, II, p. 126 (1796) : Sinclair, Hort. Gram. Wob. fol. 146 (1816) : S. F. Gray, Brit. Pl. II, p. 147 (1821). *A. vulgaris* var. β , Smith, Fl. Brit. I, p. 80 (1800). ' *A. dubia* Leers', Lam. & DC. † Fl. Fr. III, p. 21 (1805). *A. laxa* S. F. Grey, Brit. Pl. II, p. 147 (1821). *A. vulgaris* var. *canina* Sinclair, Hort. Gram. Wob. p. 271 (1824). *A. vulgaris* var. *aristata* Hook. Brit. Fl. p. 34 (1830) : Hartm. Skand. Fl. ed. 2, p. 19 (1832) : Parnell, Grass. Scot. p. 34 (1862). *A. vulgaris* var. *vinealis* ‡ Schur, Enum. Plant. Transsilv. p. 734 (1866). *A. tenuis* var. *aristata* (Parn.) Druce, Brit. Pl. List, p. 79 (1908). *A. vulgaris* var. *dubia* (DC.) Rouy, Fl. Fr. XIV, p. 64 (1931). *A. capillaris* var. *aristata* (Parn.) Druce, Fl. Oxford., ed. 2, p. 474 (1927). *A. capillaris* var. *dubia* (DC.) Druce in Bot. Exchange Club Rep. for 1928, p. 765 (1929).

Representative specimens.—K. MIDDLESEX: Teddington, *Sandwith* and *Milne-Redhead* 38. SURREY: Kew, *Turrill*; Richmond Park, *Hubbard*. WESTMORLAND: Grasmere : *Philipson* 142. B. SURREY: Field between Long Ditton and Claygate, *Britton* 744.

2. Culm long and trailing; leaves flat, broad. Panicle large, pyramidal, branches often rough. Glumes pale green. In damp humus, under shade. When grown in the open it becomes identical with the normal form.—*A. umbrosa* Schur in Oestr. Bot. Zeitschr. IX, p. 47 (1859). *A. vulgaris* var. *umbrosa* Schur, loc. cit. (1859). *A. vulgaris* var. *umbracola* Schur, Enum. Plant. Transsilv. p. 734 (1866).

Representative specimen.—K. SURREY: Box Hill, *Philipson* 149, 150.

* Withering cites *A. canina* Leers, which agrees in every respect with *A. canina* Linn. Smith and Sinclair, however, both interpret Withering's plant as *A. vulgaris* With., and certain parts of the description support this view.

† The figure given by Leers for *A. dubia* agrees best with *A. canina* without awns. *A. compressa* Willd. and *A. signata* var. *aristata* Schur are both based on *A. dubia* Leers.

‡ This plant is based on *A. vinealis* Schreb., but the description refers to *A. tenuis* Sibth. without awns.

3. Leaves lax and narrow, sometimes rolled, pale green. Culms fine. Panicle with few spikelets. In dry soil under shade. When grown in the open it becomes identical with the normal form.—‘*A. stolonifera* Linn.’ Leers, Fl. Herb. p. 20 (1789). *A. tenella* Hoffm.* Deutschl. Fl. 1, p. 36 (1800). *A. vulgaris* var. *tenella* (Hoffm.) Gaudin, Agrost. Helv. p. 84 (1811). *A. vulgaris* var. *parviflora* Schur, Enum. Plant. Transsilv. p. 734 (1866).

Representative specimens.—K. SURREY: Richmond Park, Hubbard and Summerhayes; Box Hill, Philipson 146–7. B. MIDLOTHIAN: Hawthornden, Shuttleworth.

4. Spikelets over 3 mm. in length. Moorland in Ireland, Scotland, and the north of England.

Representative specimens.—D. CUMBERLAND: Skinburness, Fox. ABERDEENSHIRE: Callater, Druce. W. INVERNESS: Aonach Mhor, Druce. KERRY: Brandon Mts., Druce as var. *grandiflora*.

Diseased states.

1. Infection with *Anguillina agrostis* (Steinbuch) Goodey. The outstanding effects of the nematode are the unequal elongation of the glumes, the elongation of the lemma and an increase in the number of its nerves, and the development of the ovary into a spindle-shaped, purple gall.—*A. vulgaris* var. *sylvatica* (Huds.) With.† Bot. Arr. ed. 3, II, p. 133 (1796); Gaud. Fl. Helv. I, p. 192 (1828). *A. vulgaris* var. δ Smith, Fl. Brit. ed. 1, I, p. 80 (1800). *A. vulgaris* var. *vivipara* Reichb. Ic. Agrost. Germ. I, p. 12 (1834).

Representative specimens.—K. CORNWALL: St. Agnes Beacon, Borlase. SURREY: Chobham Heath, Clarke. B. ESSEX: Walthamstow, Forster. No localities: ex Herb. Banks and Pulteney.

2. Infection with *Tilletia decipiens* (Pers.) Körn. The chief symptoms are the dwarf caespitose habit with numerous culms, the panicle usually compact, with undulating branches, and the glumes often shorter and broader than in healthy specimens. Throughout Britain on poor soils.—*A. pumila* Linn. Mant. p. 31 (1767); Lightf. Fl. Scot. II, p. 1081 (1777). *A. polymorpha* var. *pumila* (Linn.) Huds. Fl. Engl. ed. 2, I, p. 31 (1778); Neilr. Fl. Wein, ed. 2, I, p. 26 (1866). *A. vulgaris* var. γ Smith, Fl. Brit. I, p. 80 (1800). *Decandolia pumila* (Linn.) Bast. Fl. Maine et Loire, p. 28 (1809). *Agrostis vulgaris* var. *pumila* (Linn.) Gaudin, Agrost. Helv. p. 85 (1811). *Vilfa divaricata* var. *pumila* (Linn.) S. F. Gray, Brit. Pl. II, p. 147 (1821). *Agrostis laxa* var. *pumila* (Linn.) S. F. Gray, op. cit. p. 148 (1821). *A. alba* var. *pumila* (Linn.) Plues, Brit. Grass. p. 150 (1867). *A. tenuis* var. *pumila* (Linn.) Druce, Brit. Pl. List, p. 79 (1908). *A. capillaris* var. *pumila* (Linn.) Druce in Bot. Exchange Club Rep. for 1927, p. 423 (1928).

* Based on *A. stolonifera* Leers.

† The specific name *A. sylvatica* was applied by Hudson to a diseased state of *A. stolonifera*; when the disease was found in *A. tenuis* Sibth. the name was applied to it, or it was reduced to varietal rank.

Representative specimens.—**K.** SUSSEX : Amberley, *Salmon*. MIDDLESEX : between Twickenham and Hounslow, *Lambert*. **B.** SOMERSET : Blackdown, *Thompson*. HEREFORD : Moccas Hills, *Ridley*. **W.** MAYO : Mallaranny, *Marshall*.

Var. *HUMILIS* (*Aschers. & Graebn.*) *Druce*, Brit. Pl. List. p. 79 (1908).

Plants low, forming a loose turf, usually with extensive underground rhizomes, which may frequently branch ; stolons absent. Culms usually not over 15 cm. high. Ligule of sterile shoots very short. All the leaves usually stiff and closely rolled, often deeply tinged with purple. Panicle usually narrow and spike-like, sometimes more diffuse. Lemma frequently 5-nerved, a dorsal awn sometimes present. On sand, inland and by the sea, and stony ground.

Type.—No type was indicated by Ascherson and Graebner.

Synonymy.—*A. vulgaris* var. *humilis* *Aschers. & Graebn.* Syn. II, p. 181 (1899). *A. vulgaris* var. *curvata* *Hack.* ex *Linton*, Fl. Bournemouth, p. 249 (1900) ; name only.

Representative specimens.—**K.** S. HAMPSHIRE : Bournemouth, *Clark* CC 129. BEDFORDSHIRE : Hatchend, *Valentine*. SHROPSHIRE : Ragleth, *Bentham*. YORKSHIRE : Kingsdale, *Milne-Redhead* and *Shaw*. W. S. HAMPSHIRE : Mudford, *Stuart*. E. ORKNEY : Black Holm, *Johnston* 4772. D. CHANNEL ISLES : Jersey, *Druce*. C. HAMPSHIRE : Christchurch Bay, *Gray*. 14 sheets have been examined.

Distribution. Incompletely known ; probably throughout the British Isles in suitable localities.

4. AGROSTIS GIGANTEA Roth, Fl. Germ. I, p. 31 (1788).

Diagnosis.—Palea $\frac{1}{2}$ length of lemma or longer ; lemma 3- or 5-nerved, rarely awned ; glumes usually smooth ; panicle remaining open in fruit ; radical leaf with its blade broadest above the base, and its ligule longer than broad, rounded ; spreading by rhizomes, sometimes also with overground stolons. Anthers 1-1.5 mm.

Description.—A perennial forming an open tuft with erect shoots or trailing with decumbent shoots, spreading underground by numerous rhizomes. Culms usually 4-8 dm., but up to 12 dm. long, erect or geniculate, often procumbent and branching at the lower nodes, green or tinged with purple below the panicle, smooth, with 5-6 brown or purple nodes. Sterile shoots not compactly tufted, the intravaginal rarely becoming elongated as stolons, the extravaginal spreading as long, often much-branched underground rhizomes, with obtuse straw-coloured or dark brown scale-leaves which split at the apex. Leaf-sheaths split to near the base, terete, striate, smooth or rough, close fitting, green or frequently tinged with purple, the sheaths of the lower nodes of the culm longer than the internodes, of the upper usually shorter. Ligule of the sterile shoots 1.5 mm. or usually longer, of the culm-leaves longer, rounded, mem-

branaceous. *Blade* up to 15 cm. long, and 8 mm. broad, broadest above the base, rolled in the bud, usually grey-green or green, often very rough on both surfaces, strongly furrowed above, flat. *Panicle* up to 25 cm. long, erect, pyramidal or cylindrical, spreading, the spikelets of adjacent verticils distinct; in fruiting the main branches remain spreading and the branchlets close against them; rhachis straight, its upper internodes rough, reddish purple or green, first or second internode the longest, up to 6 cm. long; branches semi-vermicillate, up to 12 cm. long, triangular, rough or rarely smooth, the main branches dividing at $\frac{1}{3}$ to $\frac{1}{2}$ their length, striate; branchlets usually in unequal pairs, rough; pedicels rough. *Spikelets* lanceolate. *Glumes* 2-3 mm. long, the lower slightly the longer, lanceolate, with acute apices, green or, more usually, purple, colourless at the apex and margins, the keel of the lower glume toothed on the upper half at least, of the upper glume less strongly toothed; the hairs of the callus short. *Lemma* $\frac{2}{3}$ the length of the glumes, broadly ovate when flattened, truncate, with a slight scabridity towards the base, 3- or 5-nerved, the two marginal nerves shortly excurrent, usually with a minute lobe between each and the mid-nerve, into which the inner lateral nerves run when present, the mid-nerve usually ending blindly beneath the apex, or excurrent as a short mucro or occasionally as a long bent awn. *Palea* $\frac{1}{2}$ - $\frac{2}{3}$ the length of the lemma, bifid, faintly 2-nerved. *Lodicules* about 0.4 mm. long. *Anthers* 1.0-1.5 mm., frequently tinged with purple. *Ovary* ovoid, about 0.5 mm. long. *Caryopsis* about 1.1×0.38 mm.

Type.—Roth's specimen is in the Herbarium of the Botanical Museum, Berlin.

Distribution.—Europe (except the north), central and southern Russia, China, Japan, North America; introduced into Australia and New Zealand. Throughout the British Isles from the Channel Isles to the Orkneys.

Flowering period.—From late June until August. Maximum in mid-July.

Var. RAMOSA (Gray) Philipson, comb. nov.

Plants with culms procumbent and branching below. The sterile shoots often extensively trailing as stolons. Panicle usually much branched, with very numerous spikelets. Woods and banks in damp loam, often in damp or shaded arable land.

Type.—No specimens have been preserved.

Synonymy.—*A. gigantea* Roth, Fl. Germ. 1, p. 31 (1788); Gaudin, Agrost. Helv. p. 81 (1811). '*A. alba* Linn.'* With. vars. 2, 3, and 4, Bot. Arr. ed. 3,

* *A. alba* Linn. Sp. Pl. ed. 1, 1, p. 63 (1753) is based on 'Agrostis panicula laxa, calycibus membranaceis muticis aequalibus' of Royen (Lugdb. p. 59; 1740), who cites 'Gramen nemorosum, paniculis albis' of Vaillant (Bot. Paris (1727), pl. 17, fig. 5). This figure is undoubtedly of *Poa nemoralis* Linn. Later authors have applied the name to species of *Agrostis*, but as the distinction between *A. stolonifera* Linn. and *A. gigantea* Roth, has not always been upheld, and as the descriptions are usually very incomplete, it is not always possible to determine to what plant it has been applied. Many of the synonyms cited here under *A. gigantea* include part of *A. stolonifera*.

π, p. 130 (1796); Sinclair, Hort. Gram. Wob. p. 342 (1824). *A. varia* Host ex Bess. Fl. Gal. Austr. I, p. 68 (1809). *A. sylvatica* Host ex Bess. loc. cit. (1809), non Huds. *A. diffusa* Host ex Bess. loc. cit. (1809). *A. decumbens* Host, Gram. Austr. IV, p. 31 (1809). ‘*A. stolonifera* Linn.’ Host, op. cit. p. 32 (1809). *Vilfa gigantea* (Roth) Beauv. Agrost. p. 181 (1812). *V. alba* S. F. Gray, Brit. Pl. II, p. 145 (1821), with the varieties *conferta*, *ramosa*, and *nuda*. *Agrostis alba* var. *major* Gaud. Fl. Helv. I, p. 189 (1828)*. *A. alba* var. *gigantea* (Roth) Meyer, Chlor. Hanov. p. 655 (1836). ‘*A. alba* var. *stolonifera* Smith’, Meyer, loc. cit. (1836)†. *A. vulgaris* var. *gigantea* (Roth) Meyer, loc. cit. (1836), in synon. *A. stolonifera* var. *gigantea* (Roth) Koch, Syn. Fl. Germ. ed. 1, p. 781 (1837). *A. alba* var. *vulgaris* Meyer, Fl. König. Hanov. III, sig. 22 (1842). *A. alba* var. *genuina* Godr. Fl. Lorraine, ed. 1, III, p. 138 (1844). *A. vulgaris* var. *stolonifera* Buckman ‡, Brit. Grass. p. 38 (1858). *A. vulgaris* var. *sylvatica* (Host) Schur in Oestr. Bot. Zeitschr. IX, p. 46 (1859). *A. flava* Schur, loc. cit. (1859). *A. signata* var. *flava* Schur, loc. cit. (1859). *A. signata* var. *gigantea* (Gaud.) Schur, op. cit. p. 48 (1859). *A. signata* var. *varia* (Host) Schur, op. cit. p. 48 (1859). *A. signata* var. *decumbens* (Host) Schur, op. cit. p. 48 (1859). *A. polymorpha* var. *diffusa* (Host) Neirl. Fl. Wein, ed. 2, I, p. 27 (1868). *A. alba* var. *alba* Thurb. § ex S. Watson, Bot. Calif. II, p. 271 (1880). *A. alba* var. *compressa* Aschers. & Graebn. || Syn. Mittel-europ. Fl. II, p. 173 (1899). *A. alba* var. *flava* (Schur) Aschers. & Graebn. op. cit. p. 174 (1899). *A. alba* var. *diffusa* (Host) Aschers. & Graebn. op. cit. p. 174 (1899). *A. alba* var. *sylvatica* (Host) Aschers. & Graebn. op. cit. p. 174 (1899). *A. alba* var. *Hostiana* Rouy, Fl. Fr. XIV, p. 61 (1913). *A. stolonifera* var. *major* (Gaud.) Farw. in Mich. Acad. Sci. Rep. XXII, p. 351 (1919).

Figures.—Host, Ic. Gram. Austr. IV (1809), pls. 54–58 : Sinclair, Hort. Gram. Wob. (1824), facing p. 342 : Meyer, Fl. König. Hanov. III (1842), pl. 8.

Representative specimens.—**K. SURREY** : Box Hill, Philipson 210 ; Mortlake, Sprague ; between Byfleet and Pyrford, Gilmour, Turrill, and Williams ; Oxshott, Philipson 231. **HERTFORDSHIRE** : Hadley Wood, Hubbard G 57. **B. HAMPSHIRE** : Highfield, Southampton, Rayner. **SURREY** : Richmond, Manor Road, Jackson. **GLOUCESTER** : Bristol, Thompson. **E. ORKNEY** : Sanday, Johnston 3304 C. **D. ESSEX** : Dovercourt, Sherrin. **HEREFORDSHIRE** : Hildersley, Pearson. **KINCARDINE** : Maryculter, Boswell. 35 sheets have been examined.

Distribution.—This grass has not been clearly distinguished from *A. stolonifera* Linn. by British botanists so that very little is known of its distribution.

* Gaudin cites *A. gigantea* Gaud. in synonymy with this name, stating that *A. gigantea* Roth, differs in the more spreading panicle and the more frequently awned spikelets.

† The figure shows Meyer to have applied this name, in error, to *A. gigantea*.

‡ Called Black Quitch, and described as having rhizomes, but probably includes *A. stolonifera* var. *stolonifera*.

§ Includes *A. stolonifera*.

|| The description does not agree with the citation of *A. compressa* Willd.

It was evidently abundant in the time of Withering, and is probably present in all the lowland districts of the British Isles.

Var. DISPAR (Michx.) Philipson, comb. nov.

Plants with culms erect or geniculate. The sterile shoots erect or shortly procumbent as stolons. Panicle variable, but frequently with few branches, bearing rather scattered spikelets. On waste land and as a weed in arable land.

Type.—The specimen of Michaux is in the Herbarium of the Muséum National d'Histoire Naturelle, Paris.

Synonymy.—*A. repens* Curtis, Obs. Brit. Grass. ed. 2, p. 35 (1790); Sinclair, Hort. Gram. Wob. folio 230 (1816). *A. nigra* With.* Bot. Arr. ed. 3, II, p. 131 (1796). *A. dispar* Michx. Fl. Bor.-Amer. I, p. 52 (1803). *A. seminuda* Knapp †, Gram. Brit. p. 115 (1804). *Vilfa dispar* (Michx.) Beauv. Agrost. p. 181 (1812). *V. nigra* (With.) S. F. Gray, Brit. Pl. II, p. 145 (1821). *V. divaricata* (Hoffm.) S. F. Gray, loc. cit. (1821). *Agrostis vulgaris* var. *seminuda* Knapp ex S. F. Gray, op. cit. p. 147 (1821), in synon. *A. alba* var. *dispar* (Michx.) A. Wood, Class-book Bot. U.S. & Canada, p. 774 (1861). *A. vulgaris* var. *nigra* (With.) Druce, Fl. Berks. p. 562 (1897). *A. tenuis* var. *nigra* (With.) Druce, Brit. Plant List, p. 79 (1908). *A. capillaris* var. *nigra* (With.) Druce, Comital Fl. Brit. p. 350 (1932). ‘*A. alba* Linn.’ Hitchcock, Manual Grass. U.S. p. 331 (1935).

Figures.—Dodonaeus, Stirp. Hist. Pempt. (1583) p. 548; Knapp, Gram. Brit. (1804), pl. 115; Bagnall in Journ. Bot. xx, (1882), pl. 227; Malte in Rep. Nat. Mus. Canada for 1926 (1928), fig. 1; Hitchcock, Manual Grass. U.S. (1935), fig. 665.

Representative specimens.—**K. HAMPSHIRE**: Sherfield English, Goddard. **ESSEX**: Dagenham Dock, Melville. **CAMBRIDGESHIRE**: Quy, Philipson 215; Chesterton, Philipson 218, 226. **OXFORDSHIRE**: between Woodstock and Shipton, Montford, Summerhayes, and Turrill 2248. **WORCESTERSHIRE**: Malvern Wells, Towndrow. **CARDIGAN**: Aberystwyth, Hubbard 1762. **DURHAM**: Bishop Auckland, Clouston 346. **FIFE**: Balmuto, Boswell. **B. SURREY**: Dorking, Groves. **WARWICKSHIRE**: Berkswell, Bagnall. **HEREFORDSHIRE**: Wellington College, Sutton. **CHESHIRE**: Heatley, Holt. **W. GLAMORGAN**: Cardiff, Vachell. **LANCASHIRE**: Abbeystead, Wheldon. **E. WORCESTERSHIRE**: Newland, Bickham. **D. OXFORDSHIRE**: Dorchester, Druce; waste ground, no locality, Druce in 1909. **GLAMORGAN**: Port Talbot,

* The references to Scheuchzer and Leers are in error. This species is probably based on a specimen in the British Museum collected by Stokes (who had collaborated in the second edition) in 1791, i.e. before the publication of the third edition. The label bears the following note:—‘This summer (1791) I discovered that there are two kinds of couch grass (called squitch or scutch etc.). These are *Triticum repens* as mentioned in English botanical works, and *Agrostis capillaris*’ (erased in different ink to *vulgaris*). ‘The *Agrostis capillaris*’ (also erased) ‘is the couch grass of ploughed fields, which gives the farmer so much trouble to extirpate. Johnathan Stokes.’

† The description and figure agree with *A. nigra*, but a specimen apparently sent by Knapp to H. Davies, now in the British Museum, is of *A. tenuis* With.

Druce. WARWICKSHIRE : Kenilworth, *Bagnall*. STAFFORDSHIRE : Alstonfield, Pearson. C. CHANNEL ISLES : Guernsey, *Marquand*. WARWICKSHIRE : Berkswell, *Bagnall*. 112 sheets have been examined.

Distribution.—Throughout England, but not completely known. Recorded from Monmouth, Glamorgan, Caernarvon, Denbigh, and Anglesey in Wales, and from Midlothian, Fife, Perth, Forfar, and Inverness in Scotland.

5. AGROSTIS STOLONIFERA Linn. Sp. Pl. ed. 1, 1, p. 62 (1753).

Diagnosis.—Palea $\frac{1}{2}$ the length of the lemma or longer; lemma 5-nerved, rarely awned; glumes smooth or slightly rough; panicle closing in fruit; radical leaf with its blade broadest above the base, or linear, and its ligule rounded; usually spreading by overground stolons, rhizomes absent. Anthers 1-1.5 mm. long.

Description.—A perennial of very variable stature. Tall or low trailing plants or forming a compact turf, spreading by overground stolons. Culms from 1-14 dm. long, geniculate-erect, or frequently procumbent and branching and rooting at the lower nodes, green or tinged with purple, smooth, with 4-5 nodes. Sterile shoots numerous and tufted or very few, the intravaginal frequently becoming elongated as often very widely creeping stolons, the extravaginal at once ascending, with only 2-3 scale-leaves at their base. Leaf-sheaths split to near the base, terete, striate, smooth or slightly rough, rather loose-fitting, green or frequently tinged with purple, the sheaths of the lower nodes of the culm longer than the internodes, of the upper about equal in length. Ligule of the sterile shoots 1 mm. on very small leaves, or usually longer, of the culm-leaves longer, rounded, membranaceous. Blade from 0.8-20 cm. long and 0.5-8 mm. broad, usually broadest above the base, rolled in the bud, pale to dark green, glaucous or purple, rough on both surfaces, furrowed above, lax or sometimes rigid, flat or rolled. Panicle 1-30 cm. long, erect, pyramidal or cylindrical, the branches spreading horizontally during flowering, the spikelets of adjacent verticils distinct, in fruiting the branches of all or all but the lowest verticils raised against the rachis, with the branchlets closed against them; rachis straight, rough or smooth, green or purple, first or second internode longest, up to 5 cm. long; branches semi-verticillate, up to 11 cm. long, triangular, rough or smooth, the main branches dividing at $\frac{1}{3}$ - $\frac{1}{2}$ their length, straight, usually several short branches in each verticil, branchlets usually in unequal pairs, rough or smooth; pedicels rough or rarely smooth. Spikelets lanceolate. Glumes 1.75-3 mm. long, the lower slightly the longer, broadly or narrowly lanceolate, with acute apices, green or more usually tinged with purple, frequently colourless at the apex and margins, smooth or minutely rough, the keel of the lower glume toothed on the upper half at least, of the upper glume less strongly toothed, the hairs of the callus short. Lemma about $\frac{2}{3}$ the length of the glumes, broadly ovate when flattened, truncate, with a slight scabridity towards the base, 5-nerved, the marginal nerves usually shortly excurrent, and a minute lobe usually opposite each

inner lateral nerve, the mid-nerve usually ending blindly beneath the apex or excurrent as a short mucro or occasionally as a long bent awn. *Palea* $\frac{1}{2}$ – $\frac{3}{4}$ the length of the lemma, bifid, faintly 2-nerved. *Lodicules* up to 0·5 mm. long. *Anthers* 1–1·5 mm. long, sometimes tinged with purple. *Ovary* ovoid, about 0·4 mm. long. *Caryopsis* about 1·0 by 0·4 mm.

Type.—There are two specimens written up as *A. stolonifera* in the Linnaean Herbarium; and since the number of *A. stolonifera* is underlined in Linnaeus's own copy of the *Species Plantarum*, he probably had a specimen of this plant at the time of publication. One specimen having a reference to Allioni's *Flora Pedemontana* (1785) cannot have been written up until after the publication of the *Species Plantarum*. It was, therefore, probably the other specimen which he had in 1753. This specimen is referable to *A. semiverticillata* Christens. It does not agree with Linnaeus's definition of *A. stolonifera*, and cannot be accepted as the type. There is apparently no type-specimen of this species in existence, and the species is here interpreted from the synonyms cited by Linnaeus*, all of which refer to a plant agreeing with his definition.

Distribution.—Throughout Europe, central Asia, reaching Siberia, Japan, and North America. Introduced into New Zealand, Australia, the Cape, and the Falklands. Throughout the British Isles, especially in lowlying districts; Channel Islands.

Flowering period.—From July until August. Maximum in mid-July.

Var. STOLONIFERA (*Linn.*) Koch, Fl. Germ. et Helv. ed. 1, p. 781 (1837).

Innovations numerous, forming a tuft at the centre of the plant, and frequently a close turf. Leaves close together on the stolens, with short blades (0·8–8 cm.). Culms usually several on a plant, low (1–2·5 dm. above the ground). Panicle short (1–10 cm.), usually dense, pyramidal or cylindrical, frequently lobed.

Type.—The variety was based on the Linnaean species.

Synonymy.—*A. stolonifera* Linn. Sp. Pl. ed. 1, 1, p. 62 (1753) : Huds. Fl. Angl. ed. 1, p. 27 (1762) : With. Bot. Arr. ed. 1, 1, p. 42 (1776) : Knapp, Gram. Brit. p. 116 (1804) : S. F. Gray, Brit. Pl. II, p. 145 (1821) †. *A. polymorpha* var. *stolonifera* (*Linn.*) Huds. op. cit. ed. 2, 1, p. 31 (1778). *Decandolia stolonifera* (*Linn.*) Bast. Fl. Maine et Loire, p. 29 (1809). *Agrostis alba* var. *stolonifera* (*Linn.*) Smith, Eng. Fl. I, p. 93 (1824) : Meyer, Chlor. Hanov. p. 655 (1836). *A. vulgaris* var. *stolonifera* (*Linn.*) Meyer, op. cit. p. 157 (1836) : Koch, Fl.

* There are three citations. The first, up to the word 'ventricosa', is taken from Linnaeus's *Flora Suecica*, p. 23 (1745), sp. 61; the remainder, i.e. 'flosculis muticis' Roy. lugdb. 59. Fl. Suec. 62', has been copied in error from sp. 62, and should read 'Fl. Suec. 61'. The definition in the *Flora Suecica* is a modification of that of Royen in *Flora Leydenensis*, p. 59 (1740), sp. 2, to which the second citation of the *Species Plantarum* refers. The third citation is to Scheuchzer, whose description is good, and who refers to a figure originally given by Lobel (1581).

† *A. pubescens* Gray, op. cit. p. 148 (1821), is perhaps a variation of *A. stolonifera* with rough glumes, but the description is not sufficiently complete to diagnose the plant.

Germ. et Helv. ed. 1, p. 782 (1837). *A. stolonifera* var. *prorepens* Koch, op. cit. ed. 2, p. 902 (1844). *A. signata* var. *genuina* Schur in Oestr. Bot. Zeitschr. IX, p. 46 (1859). *A. signata* var. *prorepens* Schur, loc. cit. (1859). *A. vulgaris* var. *repens* Schur, loc. cit. (1859). *A. vulgaris* var. *prorepens* Schur, Enum. Plant. Transsilv. p. 734 (1866), in synon. *A. alba* var. *prorepens* (Koch) Aschers. & Graebn. Syn. Mittel-europ. Fl. II, p. 175 (1899).

Figures.—Lobel, Kruydtboeck (1581), p. 21 : Knapp, Gram. Brit. (1804), pls. 27 and 116 (1824) : Sinclair, Hort. Gram. Wob. facing p. 346 : Reichb. Agrost. Germ. I (1834), figs. 1431 and 1436 : Lowe, Brit. Grass. (1858), pl. 17 B : Jansen & Wachter in Nederl. Kruid. Archiv. (1933), pp. 149 & 152.

Representative specimens.—See under each ecad. 730 sheets have been examined.

Distribution.—Throughout the British Isles.

Ecas 1. STOLONIFERA (*Linn.*) Philipson, comb. nov.

Leaves about 3-4 mm. broad, flat, usually pale green, sheaths often a reddish purple. Stolons usually numerous and widely creeping. Culms becoming erect. Panicle usually dense and lobed. Growing as isolated plants as a weed in farmland, and waste places, frequent on sea-cliffs.

Type.—The ecas is based on the Linnaean species.

Synonymy.—*A. coarctata* Ehrh. ex Hoffm. Deutschl. Fl. ed. 2, I, p. 37 (1800), *A. brevis* Knapp *, Gram. Brit. p. 116 (1804). *Decandolia stolonifera* var. *coarctata* (Ehrh.) Bast. Fl. Maine et Loire, p. 29 (1809). *Vilfa coarctata* (Ehrh.) Beauv. Agrost. p. 181 (1821). *V. stolonifera* var. *brevis* (Knapp), S. F. Gray. Brit. Pl. II, p. 146 (1821). *Agrostis stolonifera* var. *angustifolia* Sinclair, Hort. Gram. Wob. ed. 2, p. 346 (1824). *A. alba* var. *coarctata* (Ehrh.) Reichb. Agrost. Germ. I, p. 12 (1834). *A. signata* var. *coarctata* (Ehrh.) Schur in Oestr. Bot. Zeitschr. IX, p. 46 (1859). *A. stolonifera* var. *coarctata* (Ehrh.) Čelak. Fl. Böhm. IV, p. 710 (1881). *A. depressa* Vasey in Bull. Torrey Bot. Club, XIII, p. 54 (1886). *A. exarata* var. *stolonifera* Vasey, loc. cit. (1886). *A. alba* var. *condensata* Hack. ex Druce in Rep. Bot. Exchange Club for 1913, p. 343 (1914). *A. reptans* Rydb. Fl. Rocky Mountains, p. 54 (1917).

Representative specimens.—K. GUERNSEY: Fermain Bay, Dawson H 2050. ISLE OF WIGHT: Blackgang, Sprague. SURREY: Headly, Fraser ; Ham, Hubbard. ESSEX: Dagenham, Hubbard, Summerhayes, and Turrill. CARDIGAN: Aberystwyth, Philipson 377, 378. SOMERSET: Berrow Church, Summerhayes G 62 A. YORKSHIRE: Richmond, Philipson 332. NORTHUMBERLAND: Tyne-mouth, Philipson 336, 338, 339. ORKNEY: Stromness, Johnston 3678. B. GLAMORGAN: Aberfam, Riddelsdell. SUFFOLK: Aldeburgh, Druce. ISLE OF MAN: Douglas Head, Holt. W. MEATH: Belvedere Lake, Dyer. W. ISLE OF WIGHT: Mersley Down, Melville. GLAMORGAN: Cardiff, Wade. E. BERWICKSHIRE: Berwick, Maclagan. ORKNEY: Johnson 2368 B. DUBLIN :

* Includes forms of *A. gigantea* as it ' throws out suckers, as is observable in all the genus '.

Dublin, Munro. **D.** HAMPSHIRE : Warnborough, Palmer 1656. MIDDLESEX : Alperton, Loydell. ESSEX : Kirby-le-Soken, Druce. CARNARVON : Nevin, Druce. FIFE : Burntisland, Templeman. SHETLAND : Fitfull Head, Druce ; Lerwick, Druce. UNST : Balta, Druce. **C.** YORKSHIRE : Richmond, Ward.

Ecas 2. *SALINA* (*Jansen & Wachter*) Philipson, comb. nov.

Leaves narrow, flat, frequently glaucous. Stolons few and usually short. Culms becoming erect. Panicle usually not lobed, often rather lax. Forming a close turf in salt marshes.

Type.—In Herbarium Jansen and Wachter ; no. 1399.

Synonymy.—*Vilfa stolonifera* var. *marina* S. F. Gray, Brit. Pl. II, p. 146 (1821). *Agrostis glaucescens* Don ex Hook. Fl. Scot. p. 26 (1821). *A. stolonifera* subvar. *salina* Jans. & Wacht. in Nederl. Kruid. Archiv. XLIII, p. 154 (1933).

Representative specimens.—**K.** KENT : Gravesend, Hubbard. SUFFOLK : Benacre Broad, Horwood. CARDIGAN : Ynys-las, Philipson 345–350. INVERNESS : Beauley, Gamble 28998. **D.** DURHAM : Castle Eden, Burdon.

Ecas 3. *ARENARIA* (*Jansen & Wachter*) Philipson, comb. nov.

Leaves short, folded, sheaths usually purple. Stolons numerous and widely creeping. Culms usually much inclined. Panicle usually dense and lobed. Glumes broad and short. Growing as isolated plants in loose sand.

Type.—In Herbarium Jansen and Wachter ; no. 1715.

Synonymy.—*A. stolonifera* var. β Linn. Fl. Suec. ed. 2, p. 22 (1755). *A. maritima* Lam. Encycl. Méth. I, p. 61 (1783). *Milium maritimum* (Lam.) Clem. Ensayo de la Vid. p. 285 (1807). *Vilfa maritima* (Lam.) Beauv. Agrost. p. 181 (1812). *Agrostis straminea* Hartm. Skand. Fl. ed. 1, p. 45 (1820). *Vilfa stolonifera* var. *maritima* S. F. Gray, Brit. Pl. II, p. 146 (1821). *Agrostis lobata* Sinclair *, Hort. Gram. Wob. ed. 2, p. 273 (1824). *A. bryoides* Dumort. Florula Belg. p. 152 (1827). *A. alba* var. *minor* With. in With. Bot. Arr. ed. 7, II, p. 157 (1830). *A. stolonifera* var. *compacta* Hartm. Skand. Fl. ed. 2, p. 19 (1832). *A. alba* var. *maritima* (Lam.), Meyer, Chlor. Hanov. p. 655 (1836). *A. stolonifera* var. *maritima* (Lam.) Koch, Fl. Germ. et Helv. ed. 1, p. 781 (1837). *A. maritima* var. *Clementei* Willk. in Willk. & Lange, Fl. Hisp. I, p. 52 (1861). *A. maritima* var. *pseudopungens* Lange in Vidensk. Medd. Kjobenh. for 1860, p. 31 (1861). *A. alba* var. *subrepens* Bab. Brit. Pl. ed. 5, p. 396 (1862). *A. salina* Dumort. in Bull. Soc. Bot. Belg. VII, p. 366 (1868). *A. alba* var. *subjungens* Hack. in H. C. Wats. Bot. Exchange Club, p. 7 (1887). *A. alba* var. *salina* (Dumort.) Richter, Pl. Europ. I, p. 43 (1890). *A. alba* var. *Clementei* (Willk.) Aschers. & Graebn. Syn. Mittel-europ. Fl. II, p. 176 (1899). *A. alba* var. *pseudopungens* (Lange) Aschers. & Graebn. loc. cit. (1899). *A. stolonifera* subvar. *arenaria* Jans. & Wacht. in Nederl. Kruid. Archiv. XLIII, p. 154 (1933).

Representative specimens.—**K.** CARDIGAN : Borth, Philipson 374–7. IRELAND : Mayo, Gamble, 27812. **B.** DEVON : Braunton Burrows, Lagan ; Northam,

* Previously published invalidly by Curtis, Obs. Brit. Grass. ed. 4, p. 36 (1804).

Forster's herbarium. **W. MERIONETH** : Harlech, *Barton*. **ARRAN** : Kildonan, *Travis*. **E. ARRAN** : Machire Bay, *Summerville*. **D. MERIONETH** : Harlech, *Barton*. **CAERNARVON** : Abersoch, *Druce*. **ANGLESEY** : Aberffraw, *Druce*. **Co. DOWN** : Strangford Lough, *Waddell*. **C. LANCASHIRE** : Hightown, *Wheldon*. **CUMBERLAND** : Maryport, *Gisbourne*. **FIFE** : St. Davids, *McT. Cowan*.

Ecas 4. CALCICOLA Philipson, ecas nov. *

Leaves flat or folded, grey-green. Stolons numerous and short or absent, and the plant caespitose. Culms erect or geniculate. Panicle narrow and meagre. Forming a close turf on chalk downs.

Type.—In the Kew Herbarium; Wiltshire: Winterbourne, *H. J. Goddard*.

Representative specimens.—**K. HAMPSHIRE**: Lobscombe Corner, *Goddard*. **SURREY**: Redham: *Philipson* 351, 352. **KENT**: Folkestone, *Gamble* 20250. **WILTSHIRE**: Winterbourne, *Goddard*; Martin, *Goddard*. **CAMBRIDGE-SHIRE**: Gog-Magog Hills, *Philipson* 357-360; Quy, *Philipson* 361, 362. **C. CAMBRIDGESHIRE**: Gog-Magog Hills, *Linton*.

Minor variations.

1. The lemma shortly awned.—*A. stolonifera* var. *subaristata* Čelak. Fl. Böhm. iv, p. 710 (1881).

A specimen of *A. stolonifera* var. *stolonifera* *ecas arenaria* has shortly awned lemmas; Cardigan: Borth, *Philipson* 366.

2. The whole plant pale yellowish green.

A single example seen; Surrey: Merstham chalk-pits, *Fraser*.

Var. **PALUSTRIS** (*Huds.*) *Farw.* in Mich. Acad. Rep. for 1919, **xxi**, p. 351 (1920).

Innovations few, with no indication of a tuft at the centre of the plant. Leaves more distant on the stolons, with longer blade (6-20 cm.). Culms usually few on a plant, higher (2-5 dm. above the ground). Panicle longer (8-30 cm.), usually narrowly pyramidal.

Type.—Hudson's specimens have not been preserved.

Synonymy.—*A. palustris* *Huds.* Fl. Angl. ed. 1, p. 27 (1762); *Hitchcock*, Manual Grass. U.S. p. 330 (1935). *A. polymorpha* var. *palustris* (*Huds.*) *Huds.* Fl. Angl. ed. 2, p. 129 (1778). *A. alba* var. 1 *With.* Bot. Arr. ed. 3, II, p. 129 (1796). *A. alba* *Smith*, Fl. Brit. ed. 1, I, p. 81 (1800). *A. mutabilis* *Knapp*, Gram. Brit. p. 28 (1804), non *Sibth.* *Decandolia alba* *Bast.* Fl. Maine et Loire, p. 29 (1809). *Apera palustris* (*Huds.*) *S. F. Gray*, Brit. Pl. II, p. 148 (1821). *Agrostis stolonifera* var. *latifolia* *Sinclair*, Hort. Gram. Wob. ed. 2, p. 225 (1824). *A. alba* var. *pallens* *Gaudin*, Fl. Helv. I, p. 187 (1828). *A. vulgaris* var. *alba*.

* Gramen estoloniferum vel stolonibus numerosis brevibus praeditum, caespites continuos in pascuis collinum calcareorum efformans; foliorum laminæ planæ vel conduplicatae, cinereo-virides; culmi erecti vel geniculati; panicula angusta et exigua.

Buckman, Brit. Grass. p. 38 (1858). *A. stolonifera* var. *flagellare* Neilr. Fl. Nieder Oesterr. p. 43 (1858). *A. densissima* Druce in Rep. Bot. Exchange Club for 1913, p. 343 (1914). *A. alba* var. *typica* Fiori, Fl. Anal. d'Ital. I, p. 97 (1923). *A. Robinsonii* Druce * in Rep. Bot. Exchange Club for 1924, p. 457 (1925). ' *A. nigra* With.' Hitchcock, Manual Grass. U.S. p. 330 (1935).

Figures.—Smith, Engl. Bot. xvii (1803), pl. 1189; and xxii (1805), pl. 1532: Knapp, Gram. Brit. (1804), pl. 28: Oeder, Fl. Danica x (1819), pl. 1623. Sinclair, Hort. Gram. Wob. (1824), facing pp. 225 and 345.

Representative specimens.—**K.** SARK: Beau Regard, *Ballard* 455, 474, 475. DEVON: Clawton, *Harvey*. HAMPSHIRE: Marchwood, *Goddard* K 2. SURREY: Ham, *Hubbard* G 57 A. MIDDLESEX: between Richmond and Twickenham, *Hubbard* G 55 A. CAMBRIDGESHIRE: Chesterton, *Philipson* 322; Cambridge, The Backs, *Philipson* 330. NORFOLK: Heacham, *Hubbard* 9250; Leziate Fen, *Hubbard* 9190. WESTMORLAND: Windermere, *Clouston* 223. NORTHUMBERLAND: Chevington, *Philipson* 369–370. ABERDEENSHIRE: Scotston, *Clouston*; Aberdeen, *Clouston* 744. **B.** HAMPSHIRE: Winchester, *Corfe* (2 sheets). GALWAY: Headford, *Shuttleworth*. **W.** HAMPSHIRE: Keyhaven, *Comber*. KENT: Smeeth, *Marshall*. MONMOUTH: Marshfield, *Wade*. NORFOLK: Thompson, *Horwood*. **E.** No locality, in arable lands, *Brodie*. **D.** HAMPSHIRE: Alton, *Vaughan*. GLAMORGAN: Port Talbot, *Druce*. PERTH: Forteviot, *Druce*. ELGIN: *Brodie*, *Druce*. **C.** KENT: Tonbridge, *Little*; Smeeth, *Marshall*. ESSEX: Walton, *Lemman*. 240 sheets have been examined.

Distribution.—Throughout the British Isles, on river banks and in ditches.

Minor variation.

With the lemma awned.—*A. stolonifera* var. *aristata* Sinclair, Hort. Gram. Wob. p. 345 (1824). *A. alba* var. *aristata* A. Gray, Manual, ed. 1, p. 578 (1848). *A. stolonifera* var. *longiaristata* Janka in Linnaea, xxx, p. 618 (1859): Plues †, Brit. Grass. p. 151 (1867).

Representative specimens.—**K.** HAMPSHIRE: Southampton, *Rayner*; *Jackson*.

Diseased states.

1. Infection with *Anguillina agrostis* (Steinbuch) Goodey. Symptoms as in *A. tenuis*.—*A. sylvatica* Huds. Fl. Angl. ed. 1, p. 28 (1762). *A. polymorpha* var. *sylvatica* (Huds.) Huds. Fl. Angl. ed. 2, I, p. 32 (1778). *A. alba* var. δ Smith, Fl. Brit. ed. 1, I, p. 81 (1800). *Vilfa alba* var. *sylvatica* (Huds.) S. F. Gray, Brit. Pl. II, p. 145 (1821). *Agrostis polymorpha* var. *vivipara* Trin. Unifl. p. 200 (1824). *A. stolonifera* var. *vivipara* Reichb. Agrost. Germ. I, p. 13 (1834).

* These supposed hybrids show no indication of *A. semiverticillata* as a parent, and can be matched with plants of *A. stolonifera* from the English coast where *A. semiverticillata* is quite absent.

† Probably includes awned forms of any species in the Sect. *Vilfa*.

Representative specimens.—**K.** SUFFOLK: Aldeburgh, Druce 9806. BUCKINGHAMSHIRE: Seer Green, Stapp. **B.** SUFFOLK: Aldeburgh, Druce. **D.** NORFOLK: Wells-next-the-Sea, Robinson 196. SUFFOLK: Aldeburgh, Druce. OXFORDSHIRE: Menmarsh, Druce.

2. Infection with *Tilletia decipiens* (Pers.) Körn. Symptoms as in *A. tenuis*.—*A. divaricata* Hoffm. Deutschl. Fl. ed. 1, 1, p. 37 (1800).

Representative specimen.—**D.** DURHAM: High Force, Druce (the lowest of the specimens).

6. AGROSTIS SEMIVERTICILLATA (*Forssk.*) Christens. in Dansk. Bot. Archiv, iv. p. 12 (1922).

Diagnosis.—Palea as long as the lemma; lemma 5-nerved, unawned; glumes rough; panicle always dense; radical leaf with its blade broadest above the base and its ligule obtuse, lacerate; spreading by overground stolons, rhizomes absent. Anthers less than 0·75 mm. long.

Description.—A perennial growing in loose tufts or with long trailing stolons. Culms 1–10 dm. long, geniculate or prostrate below, often branching and rooting at the lower nodes, finally becoming upright or inclined, greyish green or tinged with purple below the panicle, smooth, with four or more brown or purple nodes. Sterile shoots not numerous, the intravaginal often becoming elongated as stolons, the extravaginal ascending at once, with two or three crowded scale-leaves at the base, never elongating as underground rhizomes. Leaf-sheaths split to near the base, terete, striate, smooth, rather loose-fitting, greyish green or tinged purple, those of the lower nodes only slightly longer than the internodes, of the upper much shorter. Ligule 1·5–5 mm. long, truncate or obtuse, toothed, membranaceous. Blade up to 15 cm. long, usually much shorter, 2–10 mm. broad, broadest above the base, rolled in the bud, usually greyish green, sometimes tinged with purple, rough, especially above, flat. Panicle up to 15 cm. long, erect, pyramidal, lobed, dense; rachis straight, smooth or slightly rough above, green or tinged with purple; branches semi-verticillate, up to 4 cm. long, the larger branches rounded and often smooth, the smaller triangular and rough, the main branch of each verticil naked for half its length, the numerous smaller branches crowded with spikelets to the base; branchlets usually in unequal pairs, crowded with spikelets; pedicels usually rough. Spikelets lanceolate. Glumes 2–2·5 mm. long, subequal or the lower slightly the longer, broadly or narrowly lanceolate with acute apices, usually tinged with purple, but sometimes only slightly, and towards the tips, the keels of both glumes toothed, and the glumes rough, at least near the keel, spikelets readily falling off in fruit. Lemma about half the length of the glumes, broadly ovate when flattened, truncate, smooth, 5-nerved, the median, and often the laterals, running into very short teeth. Palea equal to the lemma, with two parallel nerves which reach the apex, distant from the margins. Lodicules narrow, about 0·5 mm. long. Anthers 0·5–0·7 mm. long. Ovary ovoid, about 0·3 mm. long. Caryopsis obovoid, about 0·75×0·5 mm.

Type.—In Forsskål's Herbarium, Botanical Museum of the University of Copenhagen.

Synonymy.—*Phalaris semiverticillata* Forssk. Fl. Aegypt.-Arab. p. 17 (1775). *A. verticillata* Vill. Prosp. p. 16 (1779). *A. aquatica* Pourr. in Mem. Toul. III, p. 306 (1788). *A. rivularis* Brot. Fl. Lusit. I, p. 75 (1804). *A. alba* var. *verticillata* (Vill.) Pers. Syn. I, p. 76 (1805) : Fiori, Fl. Anal. d'Ital. I, p. 97 (1923). *A. densa* M. Bieb. Fl. Taur. et Cauc. p. 56 (1808). *Decandolia stolonifera* var. *verticillata* (Vill.) Bast. Fl. Maine et Loire, p. 29 (1809). *Agrostis Villarsii* Poir. in Lam. Encyc. Méth. Suppl. I, p. 251 (1810). *Vilfa verticillata* (Vill.) Beauv. Agrost. p. 182 (1812). *Agrostis decumbens* Muehl. ex Elliot, Fl. S. Carolina and Georgia, I, p. 136 (1816). *A. stolonifera* Presl *, Cyp. et Gram. p. 22 (1820). *A. alba* var. *densiflora* Guss. Fl. Sicul. Syn. I, p. 133 (1842) ; Fiori, Fl. Anal. d'Ital. I, p. 97 (1923). *A. anatolica* Koch in Linnaea, xxI, p. 379 (1848). *A. adscendens* Lange, Pug. Pl. Hisp. in Vidensk. Meddel. Kjoebh. 1860, p. 33. *Nowodworskya verticillata* (Vill.) Nevski in Acta Inst. Bot. Acad. Sci. U.S.S.R. ser. I, p. 143 (1936).

Figures.—Trin. Spec. Gram. I (1882), p. 36 ; Reichb. Agrost. Germ. (1834), pl. xxxv, fig. 1435 : Cusin & Ansberque, Herb. de la Fl. Fr. xxiv (1874), p. 86 : Husnot, Gram. (1896-99) pl. IX.

Representative specimens.—**K. GUERNSEY** : St. Sampson's and Port Peter, Robinson. **B. GUERNSEY** : Vale, Druce. **W. GLAMORGAN** : Barry Docks, Wade. **D. CORNWALL** : Falmouth, Hamilton Davey ; Charleston, Miss Todd. **SUSSEX** : Southwick, Cottes. **STAFFORDSHIRE** : Burton, Druce. **GLAMORGAN** : Cardiff, Druce. **YORKSHIRE** : Meanwood, Leeds, Butcher. **C. CHANNEL ISLES** : Guernsey, Barton ; Evans.

Distribution.—Southern Europe, SW. Asia, N. India, N. Africa, and the Canaries. Introduced into W. France, N. and S. America, Cape Colony, and S. Australia.

An alien on waste land in southern England. Established in Guernsey. Recorded from vice-countries 1, 2, 13, 19, 39, 41, and 64.

Flowering period.—June and July.

THE HYBRIDS.

1. *A. CANINA* × *TENUIS*.

All the specimens are caespitose, with rhizomes. *Ligule* short and truncate or oblong. *Lemma* 5-nerved, awned or unawned, asperulence thinly scattered on the back. *Palea* $\frac{1}{3}$ - $\frac{1}{2}$ the length of the lemma.—*A. canina-vulgaris* Mercier in Reut. Cat. Genev. ed. 2, p. 300 (1861). *A. vulgaris* × *canina* Sanio, Verh. Bot. Brand. XXXII, p. 107 (1890) ; Murb. in Bot. Notiser, 1898, p. 10. *A. vulgaris* × *canina* a. *Sanionis* and b. *Mercieri* Aschers. & Graebn. Syn. Mittel-europ. Fl. II, pp. 191, 192 (1899).

* A specimen of *A. semiverticillata* is named *A. stolonifera* in the Linnaean Herbarium.

Specimens.—**K. HAMPSHIRE**: Lyss, Gamble in 1906. **ABERDEENSHIRE**: near Banchory, Clouston 726 b in 1934. **CORK**: Rathcormack, Bond in 1927. **W. UIST**: Shoolbred in 1891.

2. *A. CANINA* × *STOLONIFERA*.

Culms decumbent at the base. *Leaves* flat, up to 3 mm. broad; *ligule* tapering, up to 3 mm. long. *Panicle* dense, pyramidal. *Lemma* 5-nerved, scabrid on the back, awned. *Palea* minute.—*A. canina* × *stolonifera* Murbeck in Bot. Notiser, 1898, p. 9.

Specimen.—**CORNWALL**: Truro, Borlase in 1932.

3. *AGROSTIS STOLONIFERA* × *POLYPOGON MONSPELIENSIS* Desf.

A perennial with procumbent culms. *Glumes* with long awns. *Lemma* awned from the back. *Palea* shorter than the lemma. *Anthers* about 1 mm. long. This plant has usually been known as *Agrostis littoralis* With. (Bot. Arr. ed. 3, II, p. 129; 1796), or as *Polypogon littoralis* (With.) Smith (Comp. Brit. Fl. ed. 3, p. 13; 1818). But the plant Withering described and figured was *P. maritimus* Willd. (since it is an annual and the glumes are awned from near the middle, etc.). The grass to which Smith applied Withering's name is almost certainly a hybrid. It has often been considered conspecific with an annual species which ranges from Abyssinia through southern Asia to China and Japan. But recently Hubbard (Fl. Trop. Afr. x, p. 162; 1937) has revived the name *P. fugax* Nees ex Steud. Syn. Pl. Glum. I, p. 184 (1854) for the annual which also differs in being fertile, in having deciduous pedicels and in the proportions of the glumes.

Specimens.—**K. DORSET**: Littlesea, Salmon. **KENT**: Erith, Lambert. **NORFOLK**: Cley, Babington. **B. HAMPSHIRE**: Portsea Island, Trimen; Porchester, Trimen. **KENT**: Woolwich, French; Plumstead, French. **GLAMORGAN**: Cardiff Docks, Melville.

THE ALIENS.

1. *AGROSTIS MUELLERI* Presl, Bot. Bemerk. p. 120 (1844).—*A. pallida* Lam. & DC. Fl. Fr. VI, Suppl. p. 251 (1815), non With.

Diagnosis.—*Lemma* $\frac{2}{3}$ the length of the glumes, 5-nerved, awned, the lateral nerves shortly, and the marginal nerves markedly excurrent as short awns; *palea* very minute; *glumes* smooth, with acute apices; *panicle* diffuse; *leaf-blades* linear; *ligule* oblong, 1–2 mm. long; apparently growing as an annual. *Anthers* about 1·5 mm. long.

Native of southern Europe.

Specimens.—**D. EDINBURGH**: Leith, Fraser and Grierson in 1920.

2. *AGROSTIS HIEMALIS* (Walt.) Britton, Sterns & Poggenb. Prelim. Catal. p. 68 (1888).

Diagnosis.—*Lemma* $\frac{2}{3}$ the length of the glumes, 5-nerved, unawned; *palea* very minute; *glumes* slightly rough, with acute apices; panicle with long branches, naked for $\frac{2}{3}$ their length; *leaf-blades* linear; ligule tapering, 2–3 mm. long; apparently growing as an annual. *Anthers* about 0.5 mm. long.

Native of North America.

Specimens.—**K.** GLOUCESTERSHIRE: Avonmouth Docks, *Sandwith*, in 1928. **B.** MIDDLESEX: Finchley, *Cooper* in 1910. **D** and **C.** W. INVERNESS: Fessit, *Marshall*, in 1896.

3. AGROSTIS OLIVETORUM Gren. & Godr. Fl. Fr. III, p. 483 (1856).

Diagnosis.—*Lemma* $\frac{2}{3}$ the length of the glumes, 3-nerved, unawned; *palea* $\frac{1}{3}$ the length of the lemma; *glumes* smooth; panicle diffuse, delicate; *leaf-blade* linear; ligule oblong, 1–2 mm. long; caespitose, erect. *Anthers* about 1 mm. long.

Native of southern Europe. Not previously recorded from the British Isles.

Specimens.—**K.** HAMPSHIRE: Marchwood, *Goddard* K 1, in 1934. **W.** GLOUCESTERSHIRE: Clifton, *Wade*, in 1924. **D.** GLAMORGAN: Port Talbot, *Druce* 20902, in 1904.

The British specimens agree more closely with the type-specimen than do some of the type-gathering. It is probable that this species is a hybrid between *A. tenuis* and *A. canina*, for the characters are intermediate and specimens with five nerves in the lemma and awns have been seen from the type-locality. The localities, however, suggest that the British specimens are introduced. (A sheet of the type-collection is in the Kew Herbarium; France: Grasse, *Duval-Jouve*, in 1844.)

4. AGROSTIS SEMIVERTICILLATA Christens. in Dansk. Bot. Archiv, IV, p. 12 (1922).

Diagnosis.—See p. 100.

Well established in the Channel Islands; sporadic on waste land in England.

5. AGROSTIS NEBULOSA Boiss. & Reut. Diagn. p. 26 (1842).

Diagnosis.—*Lemma* $\frac{1}{3}$ the length of the glumes, 1-nerved, unawned; *palea* equal to the lemma in length; *glumes* smooth, with obtuse apices; *panicle* diffuse, with very fine branches; *leaf-blades* linear, ligule oblong, about 2–3 mm. long; annual. *Anthers* about 1 mm. long.

Native of southern Spain.

Specimens.—**K.** EDINBURGH: Slateford, *Fraser*, in 1910. **B** and **D.** OXFORDSHIRE: Osney, *Druce*, in 1913.

Frequently cultivated as an ornamental grass. Distinguished from other southern European annual Agrostides by the very short lemma.

6. AGROSTIS LACHNANTHA Nees in Ind. Sem. Hort. Bot. Vratisl. (1834).

Diagnosis.—*Lemma* $\frac{1}{3}$ the length of the glumes, 3-nerved, with hairs on the

back of the lateral nerves, unawned; *palea* very nearly equal to the lemma in length; *glumes* smooth, with acute apices; *panicle* narrow, lax; *leaf-blades* linear, ligule tapering, 3–4 mm. long; plants loosely trailing. *Anthers* about 0.75 mm. long.

Native of South Africa.

Specimens.—**K**, **D**, and **C**. SELKIRK : Galashiels, *Hayward*, in 1909.

7. *AGROSTIS AVENACEA* J. F. Gmel. Syst. II, p. 171 (1791).—*Deyeuxia Fosteri* Kunth, Rev. Gram. I, p. 77 (1829); *Agrostis retrofracta* Willd. Enum. Hort. Berol. p. 94 (1809).

Diagnosis.—*Rhachilla* produced, hairy; *lemma* about $\frac{1}{3}$ the length of the *glumes*, densely hairy, 5-nerved, awned, the lateral and marginal nerves excurrent, the latter as short awns; *palea* $\frac{2}{3}$ the length of the *lemma*; *glumes* smooth, finely tapered; *panicle* lax, branches long, naked for half their length; *leaf-blade* linear, ligule tapering, 3–4 mm. long; plants trailing. *Anthers* about 1 mm. long.

Native of Australia and New Zealand.

Specimen.—**K**. SELKIRK : Galashiels, *Hayward*, in 1909.

Recorded as *A. retrofracta* (Rep. Bot. Exchange Club for 1921, p. 548; 1922).

A. elegans Thore (S. Europe) and *A. eriantha* Hack. (S. Africa) are recorded by Druce, Brit. Pl. List, ed. 2, p. 126 (1928), but I have seen no specimens.

KEY TO THE NATIVE AND ALIEN SPECIES.

Rhachilla not produced.

Palea minute.

Anthers 1 mm. or longer.

Marginal awns of *lemma* about 0.5 mm.; annual *A. Muelleri*.

Marginal awns of *lemma* about 0.25 mm.; perennial.

Radical leaves with a single ventral groove *A. setacea*.

Radical leaves with four or more ventral grooves *A. canina*.

Anthers less than 0.75 mm. long *A. hiemalis*.

Palea more than $\frac{1}{3}$ the length of the *lemma*.

Lemma not hairy on the back.

Lemma about $\frac{2}{3}$ the length of the *glumes*, *palea* shorter than the *lemma*, *anthers* 1 mm. or longer.

Rhizomes present, *panicle* open in fruit.

Ligule of sterile shoots shorter than broad *A. tenuis*.

Ligule of the sterile shoots longer than broad.

Palea $\frac{2}{3}$ the length of the *lemma*, leaves narrow *A. olivetorum*.

Palea $\frac{2}{3}$ the length of the *lemma*, leaves broad *A. gigantea*.

Rhizomes absent, *panicle* closed in fruit *A. stolonifera*.

Lemma $\frac{2}{3}$ the length of the *glumes* or less, *palea* and *lemma* subequal, *anthers* less than 0.75 mm. long.

Lemma 5-nerved; perennial *A. semiverticillata*.

Lemma 1-nerved; annual *A. nebulosa*.

Lemma hairy on the back *A. lachnantha*.

Rhachilla produced, *lemma* hairy *A. avenacea*.

VARIATION, FLUCTUATION, AND FIXITY OF CHARACTERS.

Variations within the species.—The study of the taxonomy of a genus such as *Agrostis*, in which polymorphy is considerable and affects most characters of the plants, must be begun by gathering together into groups individuals which resemble each other closely. When it is attempted to separate these groups on absolute morphological characters it is often found to be impossible, because of the occurrence of a few plants which cannot be placed more certainly in one group than in another. These intermediate individuals indicate that we are dealing with the range of variation of a larger and more comprehensive group, of which the smaller groups are but the clustering of the individuals found in nature about some particularly favoured variation.

Fortunately this process of the 'lumping' of groups has its limits; eventually groups are found in the genus which do not show overlapping, but whose distinctness becomes more abundantly proved the more the material examined.

These well-defined groups have been treated as species and have been given binary names. Having by this process of synthesis arrived at our concept of the species in the genus, each species must be analysed to resolve it into its component varieties and minor variations. A species has been divided into two or more varieties only when these subdivisions of the species are clearly and almost constantly separable by a combination of characters. In practice the varieties can be diagnosed by the characters given in the key, but as these characters may involve differences merely of degree, in exceptional cases the naming of the variety may become uncertain by means of the key-characters alone. Under these circumstances the additional characters mentioned in the descriptions should be taken into account. It is equally important to note that the varieties are in the main ecologically distinct; in the table below are given the characteristic habitats of each of the varieties described in this paper:—

Species.	Variety 1.	Habitat.	Variety 2.	Habitat.
<i>A. canina</i>	<i>fascicularis</i> .	Damp acid soil.	<i>arida</i> .	Dry acid soil.
<i>A. tenuis</i>	<i>hispida</i> .	A variety of dry soils.	<i>humilis</i> .	Loose sand.
<i>A. gigantea</i>	<i>ramosa</i> .	Damp or shade.	<i>dispar</i> .	Dry and exposed.
<i>A. stolonifera</i> ...	<i>stolonifera</i> .	Chiefly dry alkaline soil.	<i>palustris</i> .	Damp alkaline soil.

In contrast to these well-marked varieties are the innumerable minor variations which can be found in all the species. Reference to the paragraphs on 'Variation within populations' (p. 111 forward) will indicate how numerous these variations are even among individuals of the same population; for

instance, in a sample of *A. stolonifera* var. *stolonifera* from a chalk-down no two plants were identical. It is evident that it is impracticable, if not impossible, to give names to all these variations, and names which have been given to them in the past should no longer be used.

These minor variations may appear quite at random among the individuals of a species, and then appear to be unrelated in any way to ecological conditions or geographical distribution. Several of these variations afford very easily scored and therefore convenient characters, and have frequently been used for the separation of varieties. When they are critically examined they show such fine gradations and occur in such an apparently casual way among otherwise homogeneous populations that little taxonomic significance can be given them. As an example of such a variation the length of the awn in *A. canina* is taken; awnless or almost awnless plants are found in most populations of *A. canina*, and have been referred to the variety *mutica* Gaud. The length of the awn, the height of its insertion, and the length of the lemma were measured in twelve spikelets from each of twenty gatherings of *A. canina*. When the awn was absent the height to which the mid-nerve ascends in the lemma was taken as the height of insertion. Maximum, minimum, and mean values of these measurements are set out in Table I. It is evident that the awn is very variable in length even in plants in which it is constantly present. In plants in which the mid-nerve often runs to the top of the lemma, awns are usually entirely absent, but are nevertheless sometimes present. It is difficult to understand what factors could influence the appearance of the awn in such a way.

TABLE I.—The length of the lemma, and the awn, and the height of its insertion, in twenty gatherings of *A. canina*.

(Twelve spikelets were measured from each gathering : 22 units = 1 mm.)

	Lemma.	Awn.	Insertion.		Lemma.	Awn.	Insertion.
Max.	33·0	73·0	4·0	Max.	35·0	50·0	14·0
Min.	28·0	50·0	3·0	Min.	30·0	26·0	9·0
Mean ...	29·6	63·0	3·1	Mean ...	33·3	39·4	11·1
1. Lyss, Hants. Awn always longer than lemma, insertion low.				2. Sheen, Surrey. Awn often longer than lemma, insertion below middle.			
Max.	39·0	80·0	10·0	Max.	45·0	47·0	20·0
Min.	34·0	58·0	7·0	Min.	40·0	24·0	12·0
Mean ...	36·8	69·1	8·7	Mean ...	41·9	35·2	17·0
3. Farnham, Surrey. Awn always longer than lemma, insertion low.				4. Sweethope, Northumberland. Awn usually shorter than lemma, insertion below middle.			

	Lemma.	Awn.	Insertion.		Lemma.	Awn.	Insertion.
Max.	40·0	63·0	20·0	Max.	43·0	34·0	21·0
Min.	39·0	18·0	13·0	Min.	37·0	23·0	16·0
Mean ...	39·8	45·0	15·9	Mean ...	40·3	29·5	19·5
5. Sweethope, Northumberland. Awn very variable, always present, insertion about middle.				6. Sweethope, Northumberland. Awn always present, shorter than lemma, insertion about middle.			
Max.	40·0	36·0	17·0	Max.	36·0	25·0	16·0
Min.	36·0	22·0	14·0	Min.	33·0	15·0	13·0
Mean ...	38·4	27·7	15·0	Mean ...	34·8	22·0	14·4
7. Drybedd, Cardigan. Awn always present, shorter than lemma, insertion below middle.				8. Drybedd, Cardigan. Awn always present shorter than lemma, insertion below middle.			
Max.	36·0	17·0	16·0	Max.	40·0	15·0	24·0
Min.	33·0	—	9·0	Min.	35·0	—	12·0
Mean ...	34·9	—	14·6	Mean ...	37·7	—	15·0
9. Drybedd, Cardigan. Only one short mucro, nerve not above middle.				10. Borth, Cardigan. Only one short mucro, nerve not above middle.			
Max.	40·0	82·0	13·0	Max.	33·0	60·0	12·0
Min.	35·0	66·0	9·0	Min.	28·0	22·0	8·0
Mean ...	38·6	76·4	11·2	Mean ...	30·2	43·9	9·6
11. Borth, Cardigan. Awn always longer than lemma, insertion low.				12. Borth, Cardigan. Awn usually longer than lemma, insertion low.			
Max.	41·0	29·0	20·0	Max.	42·0	—	39·0
Min.	36·0	—	15·0	Min.	36·0	—	9·0
Mean ...	38·3	—	17·0	Mean ...	39·7	—	25·6
13. Sandhurst, Hants. Awn short or often absent, nerve not above middle.				14. Oakmere, Cheshire. Awn short or usually absent, nerve often to near apex.			
Max.	40·0	—	39·0	Max.	41·0	22·0	39·0
Min.	37·0	—	12·0	Min.	38·0	—	15·0
Mean ...	38·5	—	24·9	Mean ...	39·7	—	26·0
15. Oakmere, Cheshire. Awn absent, nerve often to near apex.				16. Oakmere, Cheshire. Awn absent, nerve often to near apex.			

	Lemma.	Awn.	Insertion.		Lemma.	Awn.	Insertion.
Max.	40·0	—	38·0	Max.	43·0	31·0	28·0
Min.	35·0	—	15·0	Min.	38·0	—	7·0
Mean ...	38·7	—	22·8	Mean ...	39·0	—	16·6
17. Oakmere, Cheshire. Awn absent, nerve often to near apex.				18. Killin, Perth. Awn rarely present, short, nerve often above middle.			
Max.	34·0	62·0	10·0	Max.	39·0	69·0	10·0
Min.	30·0	46·0	8·0	Min.	37·0	53·0	7·0
Mean ...	32·0	50·9	9·0	Mean ...	38·3	60·0	8·2
19. Richmond, Surrey. Awn longer than lemma, insertion low.				20. Porlock, Somerset. Awn always longer than lemma, insertion low.			

On the other hand, the minor variations may be correlated in some way with the environment of the plants in which they are found. As an example of such a character the length of the spikelet in *A. canina* may be quoted ; this character has also been employed to separate varieties, as by Druce in this country. When abundant material was examined it became evident that there is a certain correlation between spikelet-size and geographical distribution in the British Isles. Larger spikelets become more frequent towards the north and west ; the correlation might be fundamentally an ecological one, as moorland and mountainous country is frequent in those parts of the British Isles.

In the first place the plants with large spikelets were examined morphologically to determine if any other characters were associated constantly with this one. Having by this means failed to establish the distinctness of these plants as a variety, all the available material of *A. canina*, amounting to over three hundred gatherings, was measured for spikelet-length ; and the frequency of the different lengths was plotted. The graph (fig. 1) shows a well-marked peak at the normal length of the spikelets in the southern parts of the country, but no second peak indicates the presence of a well-defined variety with longer spikelets. There seems to be a continuous series of forms, gradually becoming less numerous as the length of the spikelet increases. However, when graphs were constructed for material from selected districts, the distinction became very obvious. In the second graph (fig. 2) there are two curves, one representing the frequency of the different spikelet-lengths for all the Scottish material, the other the frequency for the south-east of England (from the Wash to Southampton Water). The latter material varies little about a strongly marked mode, whereas the Scottish material shows a much higher mode, maintains a good frequency at the upper limit of the English material, and a few plants occur with extremely long spikelets.

Although in this instance there is an undoubtedly relationship between distribution and the length of the spikelet, it does not seem possible to draw an arbitrary line of separation, for though the extremes are well defined, they are connected by a continuous series.

Since the variations may be correlated in their appearance with their environmental conditions, they would not be expected to be combined at random in the plants in nature. Combinations of characters which are unsuited to a given set of habitat-conditions may be eliminated, and a continual selection of more suited plants would result. Extremes in environmental conditions

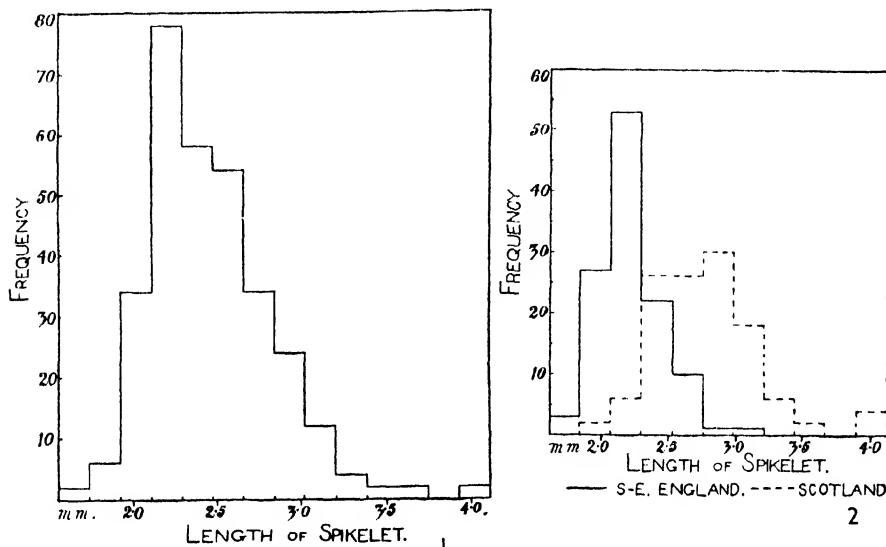


FIG. 1.—Frequency of spikelet-lengths in *A. canina* throughout the British Isles.

FIG. 2.—Frequency of spikelet-lengths in *A. canina* in Scotland and the south-east of England. Twice as many gatherings were available from the south-east of England as from Scotland, and, therefore, the Scottish frequencies have been doubled to make the graphs more comparable.

may involve more rigorous selection, and result in more uniform populations. Thus there would be formed ecological groups within the species which would be more or less distinct according as the range of habitats in which the species is able to flourish is great or small. *A. stolonifera* var. *stolonifera* is able to grow in very diverse habitats, as, for example, sand-dunes, chalk downs, salt marshes, and as a weed on farmland. In each of these habitats a distinct phenotype of the plant grows, but just as there are intermediate habitats, so there are intermediate phenotypes, and the more material of these forms that is studied, the less distinct they will appear to be. These phenotypes are in reality part of a continuous range of variation within the variety *stolonifera*, and are the result of the favouring of particular combinations of variations by particular habitats. In *A. stolonifera* var. *stolonifera* these phenotypes are sufficiently

distinct and of such economic importance as to warrant the application of names. They are given the status of ecads (Clements, 1905), but it is not meant to imply that they are of any more significance than other groups which are due to the action of the environment, but which have not had names applied to them in this revision.

Apart from this selective action, the conditions of the environment may have a more direct effect in moulding the form of the plants which grow in it. Experiments were carried out by transplanting roots of the species, not only from their typical habitats, but from as diverse situations as could be found, and growing them under uniform conditions at Kew. These transplant experiments brought to light several interesting points which are of importance in the taxonomy of these species.

The habit of the plant in most species may become profoundly influenced by the conditions of the habitat. Dampness induces increased production of stolons in stoloniferous plants, and a light soil produces a similar increase in the length of the rhizomes in rhizomatous plants. Plates 14 and 15 are photographs of two herbarium sheets of plants of *A. canina* var. *fascicularis*, one (Plate 14) from a plant growing in a very wet situation in shade, and the other (Plate 15) from the same plant after cultivation for two years at Kew. The long stolons and lax leaves have disappeared and the culms are less than $\frac{1}{2}$ the length found in the natural habitat. The influence of shade depends in part on the edaphic factors combined with it. On damp soil a lengthening or etiolation of all the parts results, but on dry soil shade only accentuates the stunting and depauperation (Plate 16). On cultivation both these forms revert to the normal habit of the species, as is shown in Plate 17, which is of the same depauperated plant of *A. tenuis* after a season's growth in the experimental plots.

Transplantation does not always bring about such great changes, even though the change in conditions may be as great. Dwarf plants of *A. tenuis* growing on very dry soil usually increase their vigour on cultivation, but the variety *humilis* when transplanted from sand retains its low habit. In the same way plants of *A. stolonifera* var. *stolonifera* transplanted from sand or chalk will increase only slightly in vigour, retaining the low habit characteristic of this variety.

While cultivation on the whole tends to make plants of a species or a variety more uniform, it is quite without power to alter those very numerous and minute differences which make the natural populations so diverse. Indeed, the very fact that such diversity can persist under such uniform conditions after so many years of natural growth proves how little any one environment can affect those variations. Such characters as the degree of roughness, coloration of the sheaths and panicle, the relative vigour of stolon and rhizome production remain constant in a given plant under cultivation. This is of very important application because by vegetative propagation it is possible for economic botanists to perpetuate the strains they have selected and be certain that the desirable qualities will be retained.

Variations within populations.

Populations were studied in the field in order to determine the nature and amount of variation that occurs under uniform natural conditions. A list of characters was drawn up and numbered (Table II), and twenty plants from

TABLE II.—List of characters used in scoring populations of *Agrostis*.

HABIT.	CULMS.
H. 1. Densely caespitose. 2. Loosely caespitose. 3. Densely matted. 4. Loosely matted.	C. 1. Numerous. 2. Few.
5. Stolons long. 6. Stolons short. 7. Stolons absent.	3. Straight. 4. Geniculate. 5. Procumbent.
8. Rhizomes present. 9. Rhizomes absent.	6. Erect. 7. Inclined.
	8. Branching at the lower nodes. 9. Not branching at lower nodes.
LEAF-SHEATH.	10. Uppermost node exserted. 11. Uppermost node inserted.
S. 1. Rough. 2. Smooth. 3. With anthocyanin. 4. Without anthocyanin.	Height in cm.
LIGULE.	PANICLE.
L. 1. Longer than broad. 2. Shorter than broad. 3. Acute. 4. Rounded or truncate.	P. 1. Ovoid. 2. Pyramidal. 3. Cylindrical. 4. Erect. 5. Nodding. 6. Diffuse. 7. Dense.
LEAF-BLADE.	Length in cm.
B. Length in cm.	Breadth in cm. (longest branch).
Breadth in mm.	
3. Broadest near base. 4. Broadest near middle. 5. Flat. 6. Rolled or filiform. 7. Medium green. 8. Pale green. 9. Greyish or glaucous. 10. Purple or reddish.	10. Contracting in fruit. 11. Not contracting in fruit. 12. Rhachis rough throughout. 13. Rhachis rough above. 14. Rhachis smooth. 15. Rhachis with anthocyanin. 16. Rhachis without anthocyanin.

TABLE III a.—Scoring of twenty plants of a population of *A. setacea*.
Bagshot, Surrey, 25 June 1934.

	H. 1	9	C. 1	3	6	9	10	30	S. 2	3	L. 1	3	B. 10	0.3	3	6	9	P. 3	4	7	6	3	10	12	16	
	1..	2..	3..	4..	5..	6..	7..	8..	9..	10..	11..	12..	13..	14..	15..	16..	17..	18..	19..	20..						
1.	1	7	9	1	3	6	9	10	28	2	3	1	3	9	0.3	3	6	9	3	4	7	7	4	10	12	16
2.	1	7	9	1	3	6	9	10	28	2	3	1	3	12	0.2	3	6	7	3	4	7	9	3	10	12	16
3..	1	7	9	1	4	6	9	10	32	2	4	1	3	10	0.4	3	6	9	3	4	7	7	2	10	12	15
4..	1	7	9	2	3	6	9	10	54	2	3	1	3	8	0.3	3	6	7	3	4	7	5	3	10	12	16
5..	1	7	9	2	3	6	9	10	20	2	3	1	3	14	0.2	3	6	7	3	4	7	7	3	10	12	16
6..	1	7	9	3	6	9	10	40	2	3	1	3	11	0.3	3	6	7	3	4	7	8	3	10	12	16	
7..	1	7	9	1	3	6	9	10	28	2	3	1	3	6	0.3	3	6	9	3	4	7	5	3	10	12	15
8..	1	7	9	1	3	6	9	10	28	2	3	1	3	6	0.3	3	6	9	3	4	7	5	3	10	12	16
9..	1	7	9	2	3	6	9	10	19	2	3	1	3	9	0.4	3	6	9	3	4	7	6	4	10	12	16
10..	1	7	9	2	4	6	9	10	20	2	3	1	3	15	0.3	3	6	9	2	4	7	9	3	10	12	15
11..	1	7	9	1	4	6	9	10	45	2	3	1	3	9	0.3	3	6	9	3	4	7	6	3	10	12	16
12..	1	7	9	1	3	6	9	10	36	2	4	1	3	10	0.3	3	6	7	3	4	7	2	10	12	15	
13..	1	7	9	1	3	6	9	10	30	2	3	1	3	10	0.4	3	6	9	3	4	7	8	2	10	12	16
14..	1	7	9	1	3	6	9	10	28	2	3	1	3	8	0.3	3	6	9	2	4	7	6	3	10	12	15
15..	1	7	9	2	3	6	9	10	15	2	4	1	3	11	0.3	3	6	7	3	4	7	9	3	10	12	15
16..	1	7	9	1	3	6	9	10	20	2	4	1	3	12	0.2	3	6	7	3	4	7	5	2	10	12	15
17..	1	7	9	1	4	6	9	10	15	2	4	1	3	6	0.2	3	6	7	3	4	7	5	2	10	12	15
18..	1	7	9	2	3	6	9	10	25	2	3	1	3	7	0.4	3	6	9	3	4	7	7	3	10	12	16
19..	1	7	9	2	3	6	9	10	20	2	3	1	3	10	0.3	3	6	7	3	4	7	6	3	10	12	16
20..	1	7	9	1	3	6	9	10	42	2	3	1	3	9	0.3	3	6	7	3	4	7	6	2	10	12	15

TABLE III b.—Scoring of twenty plants of a population of *A. canina* var. *fascicularis*.
Richmond Park, Surrey, 1 July 1934.

	H. 3	9	C. 2	8	10	25	S. 2	3	L. 1	3	B. 4	4	1	3	5	8	2	P. 2	4	6	5	3	11	13	16	
1..	3	6	9	2	4	6	8	10	30	2	4	1	3	5	8	2	4	6	6	8	4	11	13	16		
2..	4	5	9	2	4	6	8	10	50	2	4	1	3	11	5	3	6	8	2	4	6	6	11	4	11	
3..	4	5	9	2	5	6	8	10	45	2	4	1	3	3	1	3	5	8	2	4	6	6	9	3	11	
4..	4	5	9	2	4	7	8	10	40	2	4	1	3	10	5	3	5	8	2	4	6	6	8	4	10	
5..	4	5	9	2	2	4	7	8	56	2	3	1	3	3	1	3	5	8	2	4	6	6	10	5	11	
6..	4	5	9	2	5	6	8	11	56	2	3	1	3	4	5	3	6	7	1	4	6	6	5	3	11	
7..	1	5	9	2	4	6	8	10	40	2	4	1	3	4	5	3	6	8	2	4	6	6	5	2	11	
8..	3	6	9	2	2	4	6	8	10	30	2	3	1	3	4	5	3	6	8	2	4	6	6	5	2	11
9..	3	6	9	2	2	4	6	8	10	35	2	3	1	3	13	1	3	6	8	2	4	6	6	5	3	10
10..	4	5	9	2	2	4	6	8	11	45	2	3	1	3	6	1	3	6	8	2	4	6	6	10	4	11
11..	4	5	9	2	5	7	8	10	48	2	3	1	3	6	1	3	6	8	2	4	6	6	11	5	11	
12..	2	5	9	2	4	7	8	10	30	2	3	1	3	4	1	3	5	8	2	4	6	6	5	3	11	
13..	2	5	9	2	2	4	6	8	10	24	2	4	1	3	3	5	8	2	4	6	6	4	2	11		
14..	1	5	9	2	4	6	8	10	25	2	4	1	3	5	1	3	6	7	2	4	6	6	5	2	11	
15..	4	5	9	2	5	6	8	10	40	2	4	1	3	5	1	3	6	8	2	4	6	6	8	4	11	
16..	4	5	9	2	5	6	8	10	37	2	3	1	3	10	5	3	6	8	1	4	6	6	7	3	11	
17..	3	6	9	2	5	6	8	10	24	2	4	1	3	8	1	3	5	8	2	4	6	6	6	2	10	
18..	3	6	9	2	5	6	8	10	30	2	4	1	3	3	1	3	5	8	2	4	6	6	6	3	11	
19..	4	5	9	2	5	6	8	10	36	2	4	1	3	3	1	3	5	8	2	4	6	6	6	3	11	
20..	4	5	9	2	5	6	8	10	30	2	4	1	3	3	1	3	6	8	2	4	6	6	6	3	11	

TABLE III. c.—Scoring of twenty plants of a population of *A. canina* var. *arida*.
 Richmond Park, Surrey, 1 July 1934.

	H. 1	7	8	C. 2	4	6	9	10	30	S. 1	4	L. 1	3	B. 5	4	1-0	3	5	7	P. 1	4	6	8	3-5	10	13	16		
1..	1	7	8	2	4	6	9	10	24	1	4	1	3	4	1-0	3	5	7	1	4	6	7	2-5	10	13	16			
2..				1	4	6	9	10	36	1	4	1	3	6	1-5	3	6	7	1	4	6	4	1-5	10	13	16			
3..				1	7	8	1	4	30	1	4	1	3	5	1-0	3	5	7	2	4	6	9	3-5	10	14	16			
4..				1	7	8	1	4	6	9	10	30	1	4	1	3	6	1-0	3	6	7	1	4	6	7	3-5			
5..				1	7	8	1	4	6	9	10	30	1	3	6	1	3	6	7	1	4	6	7	2-5	10	13	15		
6..				1	7	8	2	4	6	8	10	30	1	4	1	3	4	0-5	3	6	7	2	4	6	8	3-0			
7..				2	7	8	1	3	6	9	10	36	1	4	1	3	6	1-0	3	6	7	2	4	6	8	3-0			
8..				1	7	8	1	4	6	9	10	36	1	3	5	1-0	3	6	7	1	4	6	7	2-5	10	13	16		
9..				1	7	8	1	4	6	9	10	42	1	3	9	2-0	3	5	7	2	4	6	7	3-0	10	13	16		
10..				1	7	8	2	4	6	9	10	50	1	4	1	3	9	2-0	3	5	7	2	4	6	9	4-0	10	13	16
11..				2	7	8	2	3	6	9	10	24	1	4	1	3	4	1-0	3	6	7	2	4	6	6	3-0	10	13	16
12..				2	7	8	1	4	6	9	10	30	1	4	1	3	4	1-0	3	5	7	1	4	6	9	3-5	10	13	15
13..				1	7	8	2	4	6	8	10	36	1	4	1	3	4	1-0	3	6	7	2	4	6	7	3-0	10	13	16
14..				1	7	8	1	4	6	9	10	25	1	4	1	3	3	0-5	3	5	7	2	4	6	5	2-0	10	13	15
15..				1	7	8	1	4	6	9	10	22	1	4	1	3	3	1-0	3	5	7	1	4	6	4	2-0	10	13	16
16..				1	7	8	1	4	6	9	10	24	1	3	1	3	4	1-0	3	5	7	1	4	6	9	4-0	10	13	16
17..				1	7	8	1	4	6	9	10	26	1	4	1	3	4	0-5	3	6	7	1	4	6	7	2-5	10	13	16
18..				1	7	8	1	4	6	8	10	36	1	4	1	3	4	1-0	3	6	7	2	4	6	6	2-5	10	13	16
19..				1	7	8	2	4	6	9	10	30	1	4	1	3	5	0-5	3	5	7	1	4	6	8	3-0	10	13	15
20..				1	7	8	1	4	6	9	10	30	1	4	1	3	5	1-0	3	6	7	1	4	6	7	2-5	10	13	16

TABLE III d.—Scoring of twenty plants of a population of *A. tenuis*.
Richmond Park, Surrey, 12 July 1934.

	H.	2	8	2	C. 2	4	6	9	11	25	S. 2	3	L. 2	4	B. 6	1	3	6	7	P. 1	4	6	6	2·5
1..	7	7	8	1	3	6	9	11	25	2	3	6	7	7	1	4	6	11	14	11	4·0	11	14	16
2..	2	7	8	1	7	8	1	3	6	9	11	20	2	4	4	1	3	6	7	1	4	6	9	3·5
3..	1	7	8	2	6	8	2	4	7	9	11	24	2	4	5	1	3	5	10	1	4	6	5	2·0
4..	2	6	8	1	7	8	1	4	6	9	11	20	2	4	2	4	5	1	3	6	7	3·5	11	14
5..	6	1	7	8	1	4	6	9	11	20	2	4	2	4	5	1	3	6	7	1	5	6	7	2·5
6..	1	7	8	1	4	6	9	10	40	2	3	2	4	3	1	3	6	7	1	4	6	9	2·5	11
7..	1	6	8	2	6	8	1	3	7	8	11	30	2	3	2	4	3	1	3	6	10	1	4	6
8..	2	6	8	1	6	8	1	3	6	9	11	25	2	3	2	4	6	2	3	5	10	3	4	6
9..	1	6	8	1	6	8	1	3	6	9	10	34	2	4	2	4	4	1	3	6	7	1	5	6
10..	1	7	8	1	6	8	1	4	6	9	10	38	2	3	2	4	4	1	3	6	10	1	5	6
11..	2	7	8	2	5	8	2	3	7	9	11	34	2	3	2	4	6	1	3	6	7	1	4	6
12..	2	7	8	2	5	8	2	3	7	9	11	25	2	3	2	4	6	1	3	6	7	3	4	6
13..	2	7	8	2	4	6	2	4	7	9	11	24	2	3	2	4	6	1	3	6	7	3	4	6
14..	1	7	8	2	4	6	1	4	6	9	11	25	2	3	2	4	7	2	3	5	10	1	4	6
15..	1	6	8	1	6	8	1	3	6	9	11	27	2	3	2	4	5	1	3	5	7	1	4	6
16..	1	7	8	2	4	6	2	3	6	9	11	22	2	4	2	4	6	1	3	6	10	1	5	6
17..	1	6	8	2	4	6	1	4	6	9	11	30	2	3	2	4	4	1	3	5	7	1	4	6
18..	2	7	8	2	4	6	1	4	6	9	10	38	2	4	2	4	3	1	3	6	7	1	4	6
19..	1	7	8	2	4	6	1	4	6	9	11	24	2	3	2	4	4	1	3	6	7	2	1	6
20..	1	7	8	2	4	6	1	4	6	9	11	27	2	3	2	4	6	1	3	6	7	1	4	6

TABLE III e.—Scoring of twenty plants of a population of *A. gigantea* var. *dispar*.
Growing as a weed in the experimental plots, Kew, Surrey, 11 July 1934.

	H. 2	C. 1	6	9	11	65	S. 1	4	L. 1	4	B. 14	3.5	4	5	7	P. 2	4	6	16	5.5	11	13	15	
1..	2..	2	6	8	1	4	6	9	11	60	1	4	1	4	9	3.0	4	5	7	2	4	6	16	6.5
2..	2	7	8	1	4	6	8	11	50	1	4	1	4	9	5.5	4	5	7	2	4	6	13	5.5	
3..	2	6	8	1	4	6	9	10	69	1	4	1	4	6	2.5	4	5	7	2	4	6	12	3.5	
4..	2	6	8	1	4	6	9	11	50	1	4	1	4	7	3.0	4	5	7	2	4	6	17	6.0	
5..	2	6	8	2	3	6	9	11	50	1	3	1	4	11	4.0	4	5	7	2	4	6	17	6.0	
6..	4	6	8	1	4	6	9	11	50	1	4	1	4	10	5.0	4	5	7	2	4	6	18	7.0	
7..	2	5	8	1	4	6	9	11	58	1	4	1	4	8	3.0	4	5	7	2	4	6	19	5.0	
8..	2	6	8	2	4	6	8	11	56	1	4	1	4	1	4	6	2.5	4	5	7	2	4	6	19
9..	4	6	8	1	4	6	9	10	56	1	4	1	4	6	7	3.0	4	5	7	2	4	6	14	
10..	2	6	8	1	3	6	9	10	48	1	3	1	4	7	2.5	4	5	7	2	4	6	17	7.0	
11..	2	7	8	1	4	6	8	11	65	1	4	1	4	7	2.5	4	5	7	2	4	6	16	6.0	
12..	2	7	8	1	4	6	9	11	60	1	4	1	4	8	3.0	4	5	7	2	4	6	14	4.5	
13..	2	5	8	1	4	6	9	10	64	1	4	1	4	12	3.5	4	5	7	2	4	6	18	6.5	
14..	2	7	8	2	3	6	9	11	74	1	3	1	4	15	6.0	4	5	7	2	4	6	17	3.5	
15..	2	6	8	1	4	6	9	11	60	1	4	1	4	9	3.5	4	5	7	2	4	6	18	7.0	
16..	2	5	8	1	4	6	9	11	60	1	4	1	4	11	4.0	4	5	7	2	4	6	16	5.5	
17..	2	6	8	1	4	6	8	11	50	1	4	1	4	19	6.0	4	5	7	2	4	6	15	4.5	
18..	2	6	8	2	4	6	9	11	60	1	4	1	4	12	5.0	4	5	7	2	4	6	14	4.0	
19..	2	6	8	1	4	6	9	11	69	1	4	1	4	9	4.0	4	5	7	2	4	6	12	3.0	
20..	2	7	8	1	4	6	9	11	74	1	4	1	4	8	4.5	4	5	7	2	4	6	15	5.5	

TABLE III f.—Scoring of twenty plants of a population of *A. stolonifera* var. *stolonifera*.
Chalk Down, Redham, Surrey, 2 July 1934.

TABLE III g.—Scoring of twenty plants of a population of *A. stolonifera* var. *stolonifera*.
Sand Dunes, Borth, Cardigan, 5 July 1934.

	H. 4	C. 2	S. 1	L. 1	B. 2	P. 2
1..	5	9	5	7	1.0	3
2..	4	5	2	5	1.0	7
3..	3	5	9	1	4	2
4..	3	6	9	1	5	4
5..	3	6	9	2	5	7
6..	3	6	9	1	5	2
7..	4	5	9	2	5	4
8..	8	4	9	2	5	7
9..	9	4	5	7	10	1.0
10..	3	5	9	1	5	7
11..	3	6	9	1	5	2
12..	3	5	9	1	5	7
13..	3	6	9	2	5	7
14..	3	6	9	2	5	7
15..	4	5	9	2	5	7
16..	4	5	9	2	5	7
17..	4	5	9	2	5	7
18..	3	6	9	1	5	7
19..	3	6	9	1	5	7
20..	3	5	9	1	5	7

TABLE III h.—Scoring of twenty plants of a population of *A. stolonifera* var. *pulcherrima*.
On the Thames bank at Kew, Surrey, 15 July 1934.

	H. 4	C. 2	S. 1	L. 1	B. 10	P. 2	4	5	7	15	4	10	13	14
1..	5	9	7	8	10	85	1	4	18	7	4	7	14	4
2..	4	5	5	7	8	10	76	1	4	5	7	2	4	7
3..	4	5	5	7	8	11	97	1	4	4	5	2	4	7
4..	4	5	5	7	8	10	72	1	4	11	4	4	7	17
5..	3	5	2	5	7	8	10	53	1	3	1	4	5	7
6..	4	5	2	5	7	8	10	99	1	4	14	3	4	5
7..	4	5	2	5	7	8	11	90	1	4	11	4	4	5
8..	4	5	2	5	7	8	11	86	1	3	1	4	17	3
9..	4	5	2	5	7	8	10	77	1	4	1	10	4	4
10..	4	5	2	5	7	8	10	92	1	4	1	12	5	4
11..	4	5	2	5	7	8	10	99	1	3	1	4	16	5
12..	3	5	1	5	6	8	11	45	1	4	1	7	3	4
13..	3	5	1	5	7	8	11	52	1	4	1	4	7	3
14..	4	5	2	5	7	8	10	97	1	4	1	4	14	6
15..	4	5	2	5	7	8	10	92	1	4	1	12	4	4
16..	4	5	2	5	7	8	11	76	1	3	1	11	5	4
17..	4	5	2	5	7	8	10	76	1	3	1	4	18	4
18..	4	5	2	5	7	8	10	90	1	4	1	4	16	3
19..	4	5	2	5	7	8	10	80	1	4	1	10	5	5
20..	4	5	2	5	7	8	10	58	1	4	1	12	4	4

each population were scored. The characters of the spikelets were not taken into account as it was impracticable to examine these in the field. The amount of variation shown by these figures therefore falls short of that actually present, since the characters of the spikelets are also variable.

The results of the scoring of eight populations are reproduced in Table III. The apparent uniformity of the plants may be supported by a cursory glance at the tables, several of the characters being constant throughout each of the populations, but on closer study an astonishing diversity is discovered. In the case of *A. stolonifera* var. *stolonifera* growing on a chalk down (Table III, f) some of the characters, such as the shape of the ligule and of the panicle and the absence of rhizomes, are constant throughout this sample of the population. Other characters, such as the length of the stolons, the coloration of the sheath, and the length of the uppermost internode of the culm, show two alternative characters in about equal proportions. Still other characters appear only rarely in the sample—these are inclined culms, flat blades, and roughness on the rachis.

The result of this variation is that not one pair of plants is identical, quite apart from the characters which are merely measurements. This amount of variation is no doubt exceptional in the genus, but in the very stable species, *A. setacea* (Table III, a), in which only five characters were found to vary (apart from the measurements of culm, blade, and panicle), eight of the twenty plants cannot be matched exactly, and the remaining twelve are grouped into four different combinations of characters, each with three plants. That is, twelve different combinations of characters were found in twenty plants selected at random from a superficially uniform population of this well-defined and stable species. In the face of such diversity the application of names to these variations becomes an absurdity.

Parallel variation.

Many of the parts of the plants may vary in the same way in the different species. Each species may not show the whole range of variation possible, but each will have its own characteristic part of the range, which will overlap more or less extensively with the range of the other species. The following are a few of the characters which vary in the same way in different species:—

The presence or absence of the awn.

The coloration and degree of roughness of the glumes.

The shape and density of the panicle.

The length of stolons and the compactness of the innovations.

Perhaps parallel variation is most striking when two species grow together and approach each other very closely in habit. A list of six localities is given where this convergence was particularly noticeable between the two species mentioned in each case:—

Locality.	Habitat.	Species.	
Bournemouth, Hants	Sand dunes.	<i>A. stolonifera</i> var. <i>stolonifera</i> .	<i>A. tenuis</i> var. <i>humilis</i> .
Box Hill, Surrey	Leaf mould, in shade.	<i>A. stolonifera</i> var. <i>palustris</i> .	<i>A. gigantea</i> var. <i>ramosa</i> .
Ben Lawers, Perth	Alpine grassland.	<i>A. tenuis</i> .	<i>A. canina</i> .
Lobscombe corner, Wilt- shire.	Chalk down.	<i>A. stolonifera</i> var. <i>stolonifera</i> .	<i>A. tenuis</i> var. <i>hispida</i> .
Borth, Cardigan	Old sand dunes.	<i>A. stolonifera</i> var. <i>stolonifera</i> .	<i>A. tenuis</i> var. <i>hispida</i> .
Borth, Cardigan	Ditch in acid bog.	<i>A. stolonifera</i> var. <i>palustris</i> .	<i>A. canina</i> var. <i>fascicularis</i> .

Photographs are given of herbarium sheets of two of the pairs of plants, those from Box Hill (Plates 18 & 19) and Borth dunes (Plates 20 & 21). The direct effect of the environment plays its part in the production of plants with similar habits because when plants from such localities have been brought into cultivation the two species have reacted differently to the new conditions. This is, for instance, the case with plants of *A. canina* var. *fascicularis* growing in very wet places. On removal to drier soil the long stolons are lost and the resemblance to *A. stolonifera* vanishes. The convergence may, however, be deeper and more permanent than mere fluctuation due to the environment, and must in some instances be due to similar genotypic variations in the two species. This is perhaps the case in the plants of *A. tenuis* and *A. canina* from Ben Lawers which show convergence in the larger spikelets and short broad leaves ; it is certainly true of the resemblance between *A. tenuis* var. *humilis* and *A. stolonifera* var. *stolonifera* *ecas arenaria*. These two plants are found in sandy soil, and resemble each other in the low compact habit, with rolled leaves, and the narrow panicle.

It therefore appears that the different species not only show the same variations, but that these are related in the same way to the environment. This is not only true of the characters, such as stolon-production, which are obviously of ecological importance, but also of characters, such as spikelet-size, which are not so obviously of ecological significance.

Abnormalities.

A well-known, but rare, abnormality of the vegetative parts of *A. canina* consists of the plant being entirely of a pale yellow colour. There is a specimen of *A. stolonifera* var. *stolonifera* in the Kew Herbarium showing the abnormality

(Surrey : Merstham Chalk pits, *Fraser*). Sinclair (1816), p. 152, gives the following account of this mutation in *A. canina* (under the name *A. nivea*) : 'The whole plant, except the panicle, of a light straw-colour. The branches are numerous and when in flower the panicle assumes that appearance which it would have after a shower of snow, being then almost white. The above characters have remained constant after the third time raised from seed on different soils (i.e.) on light siliceous soil in Aspley Wood, where trees have been thinned ; on a heath soil, and on a clayey loam.'

Specimens of *A. stolonifera* and *A. tenuis* with leaves variegated with stripes of yellow and green are preserved at Woburn Abbey in a collection of grasses made by Sinclair in 1824.

Jansen and Wachter (in Nederl. Kruid. Archiv, XLIII, p. 153 (1933)) record plants of *A. stolonifera* var. *major* (Gaud.) Farw. (= *A. gigantea* Roth) in which the branch system of the panicle is more complex than in normal plants ; they have applied to the specimen in their herbarium the word *composita*. The main branch of each semi-verticil resembles a complete panicle, itself possessing alternate semi-verticils of branches.

I have only twice seen British specimens with a well-developed bract at the base of the panicle—on a specimen of *A. stolonifera* in Druce's herbarium (Shetland : Fitfull Head, *Druce*) and on a specimen of *A. tenuis* infected with *Tilletia* (Orkney : Hoy, *Johnston* 2637). The branches of the lowest semi-verticil are closely enwrapped by a brown scarious bract which is over 1 cm. long.

In the herbarium of Jansen and Wachter there are specimens of both *A. tenuis* and *A. canina* with well-developed branches of the panicle in the axil of the uppermost leaf of the culm. They have been written up as f. *bracteata*.

The abnormalities of the spikelets have been made the subject of a separate paper (Philipson in Journ. Bot. 1935, p. 65) ; they may be grouped under four heads, the first two of which are due to disease :—

1. Infection with *Anguillina agrostis* (Steinbuch) Goodey : *Agrostis sylvatica* Huds. The nematode produces a galled ovary with enlarged glumes and lemma. The disease has been seen in *A. stolonifera*, *A. gigantea*, *A. tenuis*, and *A. canina*. Since the publication of the paper on these abnormalities a specimen sent by Hudson to Linnaeus has been found in the Linnaean Herbarium. The specimen was unnamed by Hudson, but is no doubt from the gathering upon which he founded his species. It is a specimen of *A. stolonifera* with nematode galls.

2. Infection with *Tilletia decipiens* (Pers.) Körn. : *Agrostis pumila* Linn. The spores of the fungus are produced in the enlarged ovary and the plant is dwarfed and the panicle becomes compact. The disease has been seen in *A. stolonifera*, *A. tenuis*, and *A. canina*.

3. Proliferation. The production of leaf-like structures in the place of the lemmas has only once been seen in living material. The abnormal spikelets were on a plant of *A. stolonifera* in the experimental plots at Kew, which had been transplanted from Tynemouth, Northumberland, a year previously.

There is a specimen of *A. stolonifera* in the British Museum Herbarium (ex Herb. Thos. Moore) which shows proliferation slightly. G. F. W. Meyer (Fl. König. Hanov. III, sig. 21½; 1842) records *A. alba panicula germinante*, which is later named by Ascherson and Graebner (Syn. Mittel-europ. Fl. II, p. 174; 1899) *A. alba* var. *prolifera*. In the 'Prodromus Florae Batavae' (Nederl. Bot. Vereen. ed. 3, p. 2191; 1916) *A. vulgaris* var. *stolonifera* m. *vivipara* is recorded from Rotterdam, and Jansen and Wachter (l.c. 153) record *A. stolonifera* var. *major* f. *prolifera* from Amsterdam.

4. Two-flowered spikelets. Spikelets with rudiments of a second floret are rare in most of the species of the genus, but are found frequently in a few species. Only three instances have been met with in British material: a plant of *A. tenuis* in Hooker's herbarium (now incorporated in the general collection at Kew) which he mentioned in his 'Flora of Britain', p. 34 (1830); a plant probably of *A. canina* in the British Museum herbarium; and a plant of *A. tenuis* in Druce's herbarium (Aberdeen: Loch-na-Gar, Druce 1899), which was given the epithet forma *sesquitertia* by Hackel. Kloos (Nederl. Kruid. Archiv, 1921, p. 113) gives a two-flowered form of *A. stolonifera* the epithet *subbiflora*.

THE VEGETATIVE ANATOMY.

Introduction.—The investigation of the anatomy of *Agrostis* was undertaken to complement the work on the taxonomy of the British species of that genus. It is not intended to give an exhaustive account of the anatomy of the whole plant, but rather a comparative treatment of the characters which are most readily observed, that is, primarily the transverse sections of the root, stem, and leaf. The sections were mostly cut by hand and mounted direct in a mixture of glycerine jelly and saffranin, a rapid and semi-permanent process which is essential when very numerous sections are being cut for future comparison.

The anatomy of eight varieties, classified under five species, was investigated and compared. These varieties include all the common forms and all those of interest to the agriculturalist and horticulturalist. At least twelve plants of distinct origin of each variety were cut when investigating each part of the plant. The eight varieties are listed below:—

1. *A. setacea* Curtis.
2. *A. canina* var. *fascicularis* (Curtis) Sinclair.
3. *A. canina* var. *arida* Schlecht.
4. *A. tenuis* var. *hispida* (Willd.) Philipson.
5. *A. gigantea* var. *ramosa* (S. F. Gray) Philipson.
6. *A. gigantea* var. *dispar* (Michx.) Philipson.
7. *A. stolonifera* var. *stolonifera* (Linn.) Koch.
8. *A. stolonifera* var. *palustris* (Huds.) Farw.

The transverse section of the root.

The earliest roots and the finer branches of the later roots are monarch or diarch (fig. 3 A). The larger roots of well-developed plants have usually six

to eight groups of protoxylem and in all the species except *A. setacea* the number of protoxylem-groups rarely exceeds twelve. In *A. setacea*, however, much larger roots are found.

The xylem-groups are embedded in a ground-tissue which usually consists of very much thickened fibres (fig. 3 B). In the centre of the stele there is usually a single large duct, but there may be as many as four of these ducts, or in *A. setacea* many more (fig. 3 C). The endodermis surrounds the fibrous stele and its cells are thickened on their inner and radial walls, passage-cells being apparently absent.

There are three regions in the cortex of the root. Immediately outside the endodermis are a few layers of flat, closely fitting cells. After two or three layers the cells become spherical and are arranged in radial rows, only being

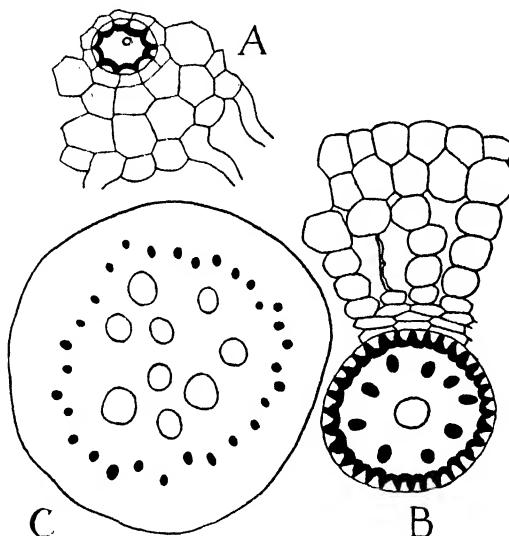


FIG. 3.—Transverse sections of roots. A, of part of a monarch root of *A. tenuis*; B, of part of a large root of *A. gigantea*; and C, the stele of a large root of *A. setacea*.

connected with other cells on their outer and inner sides. The outermost region of the cortex consists of two or three layers of large close-fitting cells, the outermost of which form the piliferous layer.

In old roots the rows of cells in the middle region of the cortex collapse, leaving the outer and inner cortex separated by a large air-space, across which stretch cellulose strands formed by the walls of the dead cells.

The roots of the various species are indistinguishable in cross-section, except in the case of the larger roots of *A. setacea*. Steles of *A. setacea* with as many as seventeen central ducts and twenty-nine xylem-groups have been examined.

The transverse section of the culm.

All sections were taken through the culm above the insertion of the uppermost leaf. In nearly all cases sections were cut near to the base, about the middle, and close to the first panicle branch, but it was found that, although higher in the culm the amount of fibrous tissue might become slightly less, the disposition of the bundles remained the same throughout.

When the culm is of small diameter the disposition of the bundles and fibres conforms to a very regular plan (fig. 5 A). The surface of the culm has regular ridges and furrows; opposite each ridge is a small vascular bundle and opposite each furrow a large bundle which runs deeper in the cortex. A ring of fibrous tissue encircles the culm, reaching the epidermis opposite each bundle, but being separated from it between them by a patch of mesophyll. At the centre of the culm the ground-tissue breaks down to form a central air-space.

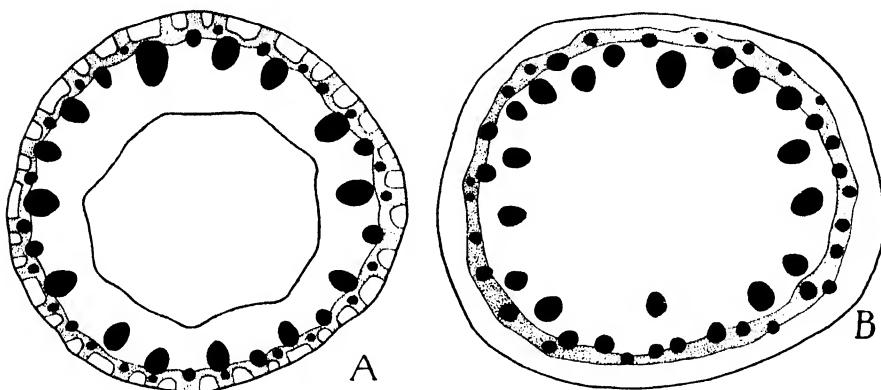


FIG. 4.—Transverse sections of : (A) a large culm and
(B) a large stolon of *A. stolonifera*.

In larger culms more bundles are present, and aberrations from the original plan are introduced (fig. 4 A). Bundles of a third order appear, alternating with the large and small bundles; in some culms there are only a few of these bundles appearing irregularly around the stem, but in very large culms they are present uniformly all round the stem. When the bundles become crowded the patches of mesophyll may be absent between them. The band of fibres becomes more clearly marked from the ground-tissue and the patches of mesophyll smaller, though it is only rarely that they are completely absent. The large bundles frequently run in the pith, unenclosed by the fibrous band, and a very small bundle may be present on their inner side running in the band of fibres. In larger culms the patches of mesophyll on each side of the largest bundles may become united so that the fibrous tissue does not reach the epidermis opposite these bundles.

The culms of all the species conform to this plan and show the same variations with size. There are no characters that can be used to separate the species, although certain types of culm are found more frequently in some species than in others. Thus the small and perfectly regular culm is found in all the species except *A. gigantea* where no small culms were found, and the character of the absence of fibres opposite the largest bundles is found most frequently in *A. stolonifera* var. *palustris* and *A. gigantea*, which most often have large culms, but is also found in all the other species.

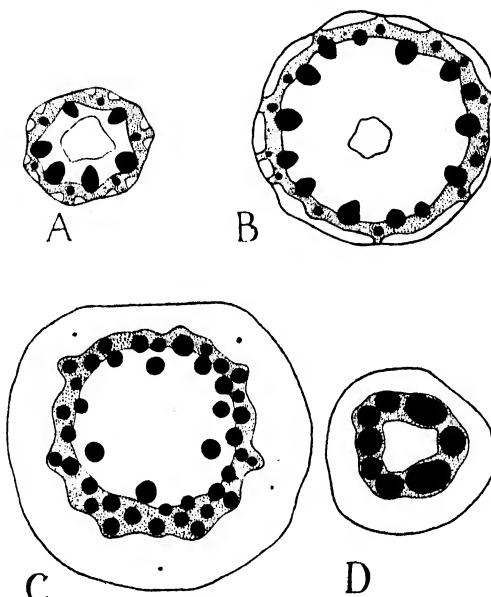


FIG. 5.—Transverse sections of: A, a small culm of *A. canina*; B, a small stolon of *A. stolonifera*; C and D, rhizomes of *A. canina*. In D the bundles are compound.

The transverse section of the stolon.

Stolons are present in all the varieties except *A. canina* var. *arida* and *A. setacea*. For cutting sections well-developed stolons were selected in which the internodes projected well beyond the leaf-sheaths, and sections were taken from internodes close to the apex and from older parts.

The arrangement of tissues is similar to that in the culm, and bundles of two or three orders alternate with a certain regularity (fig. 4 B), but the presence of leaf-traces complicates the pattern. The fibres in which the bundles are embedded may form a continuous ring as in the culm or may be present only near the bundles. The bundles are not always in so compact a ring as in the culm; the larger bundles may be scattered in the pith and the smaller in the cortex.

The pith may be solid in the younger internodes, but is usually hollow. The ground-tissue between the epidermis and the vascular tissue may be wide or narrow. In the latter case the ring of fibres if present may reach the epidermis in places, but there is no regularity in this as there is in the culm (fig. 5 B).

The stolons of all the species have their tissues arranged in this way, and there is no means of distinguishing between them.

The transverse section of the rhizome.

Rhizomes are not present in any of the varieties of *A. stolonifera*, in *A. setacea*, or in *A. canina* var. *fascicularis*. In the other species and varieties they are constantly present, but developed to very varying degrees. The transverse sections of the rhizome are very similar to those of the stolon (fig. 5 C), and in some cases it would be impossible to distinguish between them. There are, however, a number of ways in which rhizomes tend to be anatomically distinct from stolons :—

1. The epidermis is more thinly cuticularized.
2. There is usually abundant starch in the cortex and pith. (There is chlorophyll in the cortex of the stolon.)
3. The pith is more frequently solid.
4. The circle of fibrous tissue never reaches the epidermis, as it does in the culm and sometimes in the stolon.
5. Small scale-leaf-traces run in the outer cortex ; they may be reduced to a cluster of fibres.
6. The individual bundles may be large and complex (fig. 5 D).

Again, there are no characters by which the various species may be distinguished.

The foliage leaf.

The disposition of the vascular bundles in the leaf is best understood if their development is traced. This can be done most readily by taking series of microtome sections through the apices of the sterile shoots, when sections of successively older leaves are obtained. The development is very similar to that in *Deschampsia* (Philipson, 1935 b). The order of appearance of the vascular strands is median, lateral, marginal, and intermediate (fig. 6 D). No other strands may appear in the narrower leaves of *A. canina* ; and in *A. setacea* not even so many are formed, for in this species there are never more than five nerves in the blade, and usually only three. All the strands in the sheath continue into the blade, none ending in the ligule. In the larger leaves additional nerves form in the blade, fusing above the base of the blade with one or another of the bundles which enter the sheath.

The transverse section of the blade is fundamentally the same in all the species. In all cases the sections were taken from well-developed blades of sterile shoots, and cut about one-third of the length of the blade above their

base. The lower surface is more or less flat, but the upper surface is furrowed (fig. 6 A, B). In each of the ridges between these furrows a nerve runs. The arrangement is quite different from that found in *Deschampsia*, where the smaller bundles run alongside the larger and are not isolated in separate ridges. Bands of fibres run below each bundle and a similar band is usually present above. Often the fibres completely surround the bundles and reach from one epidermis to the other. Other bands of fibres are found in most leaves running along the lower surface below the furrows—that is, between the bundles. Fibres are also present at the margins of the blades. The stomata are present in longitudinal bands on each surface, but are much more numerous on the upper surface.

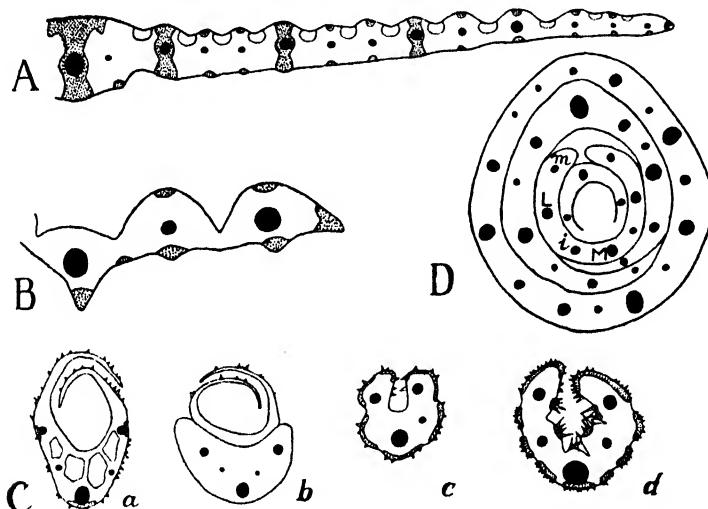


FIG. 6.—A and B, transverse sections of leaf-blades of *A. gigantea* and *A. canina* respectively. C (a, b, and c), sections through the ligule and blade of a radical leaf, (d) of the blade of a culm-leaf, of *A. setacea*. D, transverse section through the apex of a sterile shoot of *A. tenuis* showing successively older blades, the letters *M*, *L*, *m*, and *i* indicate the median, lateral, marginal, and intermediate nerves of the second leaf.

On the lower surface they are found on each side of the fibrous bands below the bundles ; on the upper surface they are found on each side of the furrows, the bottoms of the furrows being occupied by more or less bulbous motor cells.

The characters of the transverse section of the leaf-blade have been so frequently advocated as an aid to diagnosis that it was thought advisable to make a very thorough investigation of them. The material was not confined to the eight varieties listed above, but all the available smaller variations and forms were cut and the characters of each blade tabulated. Only by this means is it possible to assess the true value of these characters in the classification of this difficult genus.

A list of the characters which were taken into consideration is given, and a selection from a large number of the scorings for leaf-sections is set out in Table IV. *A. setacea* with its setaceous leaves (fig. 6 C) is so distinct that it could not be included.

Characters used in the scoring of leaf-sections.

A . . .	Mid-keel.	1. Prominent. 2. Perceptible. 3. Absent.
B . . .	Lateral keel.	4. Prominent. 5. Perceptible. 6. Absent.
C . . .	Furrows on upper surface.	7. Deep. 8. Shallow.
D . . .	Fibrous bands between the bundles.	9. Present. 10. Absent.
E . . .	Fibrous bands of marginal bundles.	11. Above and below the bundles. 12. Only below.
F . . .	Bundles in marginal ridge.	13. One. 14. Two.
G . . .	Epidermal cells.	15. Regular. 16. Irregular.
H . . .	Motor cells.	17. Well defined. 18. Ill defined.
I . . .	Stomata on lower surface.	19. Rare (0-3 per trans. sect.). 20. Frequent (4 or more per trans. sect.).
J . . .	Asperities.	21. Several. 22. Few.

From an examination of Table IV it can be seen that while some characters vary greatly within the species others are more constant. For example, two bundles in the marginal ridge are rare and asperities are rarely numerous, but the characters of the keels, ridges, and fibrous tissue may vary considerably. It is more important to note that none of the varying characters is both constant for a given species and constantly different in another. They may be more constant in one species than another, giving to each, on the average, a certain character. Thus stomata are more frequent on the lower surface of *A. stolonifera* than of *A. canina*, and the furrows are deeper in the latter species. The presence or absence of the fibrous strands between the bundles has been used to diagnose the British species of *Agrostis*, but as these strands are present in some plants and absent in others of all the species this character is worthless.

The species of *Agrostis* therefore may show differences in the frequency of occurrence of certain anatomical leaf-blade characters, but they all conform to the same plan and none of the characters investigated are diagnostic for a

TABLE IV.—The scoring of the characters of the transverse sections of the leaf-blades.

Name and plant no.	A.	B.	C.	D.	E.	F.	G.	H.	I.	J.
<i>A. stolonifera</i> var. <i>palustris</i> .										
C 2 i.....	1	5	8	9	11	13	16	18	20	22
C 2 iii.....	2	5	7	9	12	13	15	18	20	22
C 14	1	5	8	10	12	13	16	18	20	22
D 1.....	2	6	8	10	11	14	16	18	20	22
D 7.....	3	5	8	9	11	13	16	17	20	21
J 6.....	1	5	7	10	12	13	16	18	19	22
<i>A. stolonifera</i> var. <i>stolonifera</i> .										
A 14	2	5	8	10	12	13	16	18	19	22
A 16	1	5	8	10	12	13	16	18	20	22
B 11	1	5	7	9	12	14	16	18	20	22
C 19	1	5	8	10	12	13	16	18	20	22
C 21	2	6	8	10	12	13	15	18	20	22
E 2.....	1	5	8	10	12	13	16	18	20	22
<i>A. gigantea</i> .										
B 34	1	5	7	10	12	13	16	17	20	22
C 13	2	5	7	9	12	13	16	18	20	22
C 24	1	5	7	10	12	13	16	18	20	22
D 2.....	1	5	8	9	11	13	15	18	20	22
D 4.....	1	5	8	10	12	13	16	18	20	22
E 31	2	6	8	10	11	13	16	18	20	22
<i>A. tenuis</i> .										
A 1.....	1	5	8	10	12	13	15	18	19	22
A 18	2	6	7	10	12	13	16	18	20	22
B 19	1	5	7	9	12	13	16	18	19	21
C 4.....	1	5	8	10	12	13	16	18	20	22
C 6.....	2	5	7	9	12	13	16	18	19	22
D 3.....	2	5	8	9	11	13	16	18	20	22
<i>A. canina</i> var. <i>arida</i> .										
A 9	1	6	7	9	12	13	16	18	19	22
A 10	1	5	7	10	12	13	16	18	19	22
B 9	1	5	7	9	12	13	16	18	19	22
B 36	1	5	7	10	12	13	16	18	19	22
C 5	1	6	7	9	12	13	16	18	19	22
E 39	3	6	7	10	12	13	16	18	20	22
<i>A. canina</i> var. <i>fascicularis</i> .										
A 13	1	6	7	9	11	13	16	18	19	21
B 6	2	5	8	9	12	13	16	18	19	22
B 13	1	5	7	9	12	13	16	18	19	22
B 18	1	5	7	9	12	13	16	18	19	22
E 13	1	5	7	10	11	13	16	18	19	22
E 28	2	5	8	10	12	13	16	18	20	22

species. It appears therefore that in the British species of this genus the anatomy of the leaves is of no taxonomic importance, except in the separation of *A. setacea*, a species which was known to be very distinct from gross morphological evidence.

In transverse sections the young sheath is seen to be closed for the greater part of its length (fig. 7), but it becomes open and its margins overlap towards the ligule. In older leaves the sheath may become split almost to the base. These transverse sections also show that the leaf-blade is rolled in the bud in most plants, one half of the blade completely enclosing the other, an arrangement which leads to a slight asymmetry. In the smaller leaves, particularly in *A. canina* (fig. 7), the rolling is reduced to a minimum, so that one margin is just overlapped by the other, which causes the leaf to appear folded in the bud. In *A. setacea* the leaves are never rolled, as the lamina is not sufficiently developed, but even in this species the asymmetry can be detected.

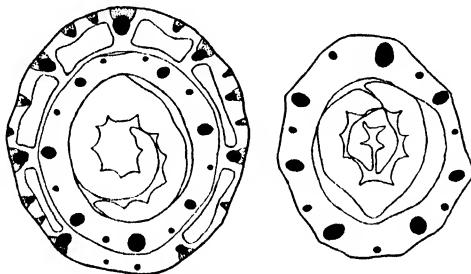


FIG. 7.—Transverse sections through sterile shoots of two plants of *A. canina*, showing the structure of the sheath and the vernation.

The bundles of the sheath show a more regular alternation of large and small bundles since the additional bundles of the blade are not present. The fibrous strands are only present on the outer side, never reaching their inner epidermis. In the sheaths of larger leaves air-spaces develop between the bundles, and these may unite above the smaller bundles.

The scale-leaf.

The scale-leaf may consist either solely of a sheath-like portion with no indication of the ligule and the blade, or it may have these regions more or less developed. When the rhizome emerges to grow as a sterile shoot, the successive leaves gradually develop a blade, unlike the leaves of an intravaginal shoot, which have strongly developed blades from the beginning of the shoot. In *A. gigantea* and *A. tenuis* the scales of well-developed rhizomes are short and obtuse, but in *A. canina* they are elongated and tapering. In the former two species the scales split at the apex with great regularity, but this is not found in *A. canina*.

A transverse section in the blade region (fig. 8 A) shows a series of alternating large and small bundles, with furrows on the upper surface between them. In the apex of most of the ridges, above the bundles, is a band of fibres, and a similar band is always present on the lower side of the bundles. These fibrous bands on the lower surface may be very broad and appear almost continuous, except for narrow breaks below the furrows. This scheme varies according as the blade is greatly or poorly developed, but its similarity to the blade of a foliage leaf is apparent.

In the sheath region the same alternation of bundles is seen (fig. 8 B). There are no additional bundles formed in the blade, as in the foliage leaf, so that the nerves of the sheath run straight into the blade without branching. Each bundle is accompanied by a band of fibres on the outer side only. The

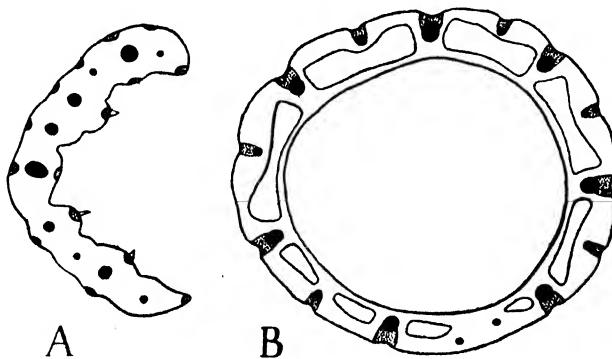


FIG. 8.—Transverse sections through a scale-leaf of *A. gigantea*.
A, through the blade, and B, through the sheath.

ground-tissue may be solid or hollow; in the latter case the cavities form between the bundles and usually unite above the smaller bundles.

The epidermis.

The culm : The epidermis of the culm shows three types of cell-arrangement in a regular sequence (fig. 9 A). Where the fibrous tissue reaches the epidermis the surface-cells also are all elongate, narrow, and thick-walled. To the outside of the parenchymatous cortex the epidermis consists of rows of large cells and stomata in regular alternation. The stomata of one row are opposite the large cells of the adjacent row. Between these two types of epidermis a transitional arrangement is seen in which rather narrow long cells alternate with small cells, which take the place of the stomata.

The stolon : The cells of the epidermis of the stolons are usually very regularly arranged (fig. 9 B). They are in longitudinal rows with very long cells alternating with short cells. Sometimes the small cells are not present between all of the long cells. Stomata occasionally replace the small cells,

and their large size disarranges the regularity of the cells around them. Bands of narrow cells are not so frequent as in the culm, as the fibres of the cortex do not so often reach to the epidermis.

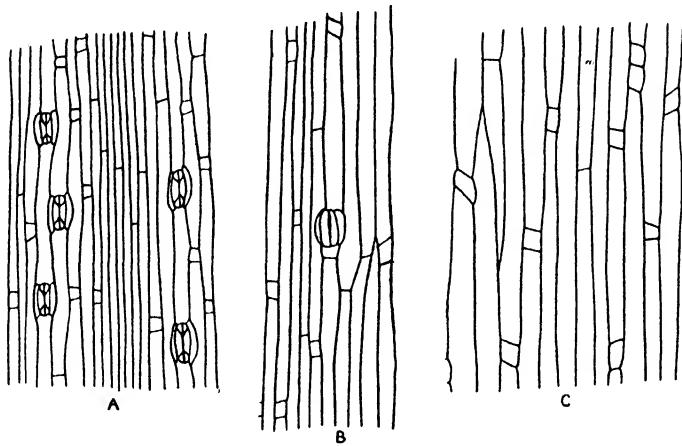


FIG. 9.—Surface-view of epidermal cells of *A. gigantea*. A, from the culm ; B, from the stolon ; and C, from the rhizome.

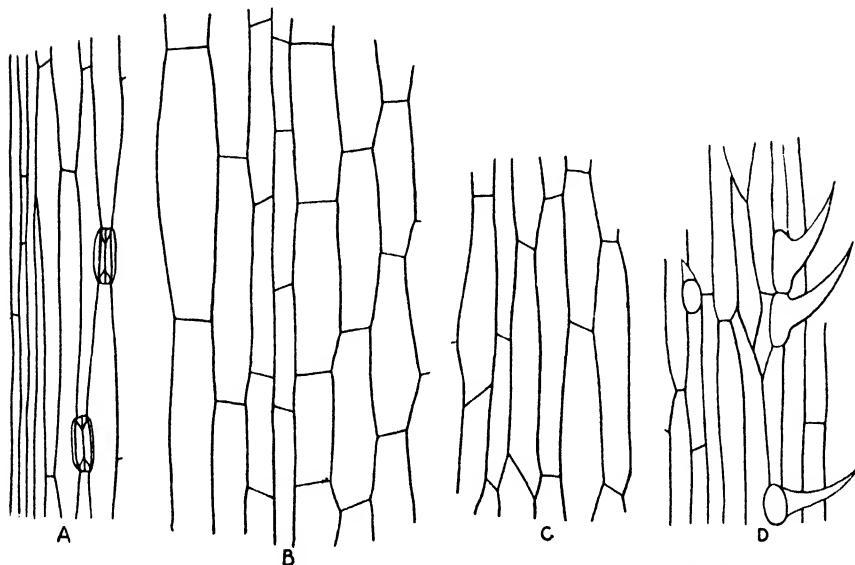


FIG. 10.—Surface-view of epidermal cells of *A. gigantea*. A, on the upper surface of the blade ; B, on the inner surface of the leaf-sheath ; and C and D, on the inner and outer surfaces of the ligule.

The rhizome : The epidermal cells of the rhizome are arranged as in the stolons (fig. 9 C), but their walls are thinner and the cells are relatively broader.

As can be seen from the figure, the regularity of the arrangement is not so strictly adhered to as in the stolons.

The leaf : The epidermis of the leaf-blade resembles that of the culm, in that bands of narrow cells alternate with bands of broader cells below the parenchyma (fig. 10 A). In the latter, large cells alternate with stomata, but the transitional type of arrangement found in the culm between these two bands is absent, as the small cells are not found alternating with the large cells in the epidermis of foliar structures. The upper and lower epidermis of the blade scarcely differ when the furrows of the upper have been flattened, except that stomata and asperities are more frequent on the upper surface.

The outer surface of the sheath resembles the lower surface of the blade. The inner surface of the sheath is devoid of stomata and consists of bands of long narrow cells alternating with bands of long and broad cells (fig. 10 B).

Both surfaces of the ligule have a very irregular cell-arrangement. The inner surface consists entirely of long cells (fig. 10 C), but on the outer surface numerous curved teeth are formed from short cells which make the arrangement even more irregular (fig. 10 D).

The epidermis of the scale-leaves differs chiefly in the rarity of the bands of narrow cells, which results from the fibres infrequently reaching the surface. Both surfaces therefore consist of regularly arranged large cells with rarely a few stomata on the outer surface.

Conclusions.

A review of the preceding account of the gross anatomy of the British species of *Agrostis* leads to the conclusion that this means of investigation is totally inadequate as a means of taxonomic identification. Apart from the structure of the root and leaf in *A. setacea*, no section of any part of the plant could be referred with any certainty to its species. It is true that the species have certain characters, of the culm and leaf for instance, that occur most frequently in them, but in no case have these characters been found truly diagnostic. The species all seem to be built to the same plan and show parallel variations about modes which are different for different species.

LIFE-HISTORIES.

Imbibition.

Approximate dimensions of the caryopses in each species are given at the end of the descriptions in the taxonomic section. The first stage of germination is the imbibition of water into the grain and a consequent increase in size. The following table, in which the average dimensions in mm. of ten grains from a plant of each species are given when dry and after twenty-four hours of imbibition, illustrates the order of this increase. The measurements were taken to within 1/100th of a mm. by means of a micrometre eye-piece, using the low power of the microscope :—

Species.	Before imbibition.			After imbibition.		
	Length.	Breadth.	<i>l/b.</i>	Length.	Breadth.	<i>l/b.</i>
	1.435	0.372	3.05	1.555	0.440	3.52
<i>A. setacea</i>	1.132	0.358	3.16	1.192	0.404	2.95
<i>A. canina</i>	1.007	0.362	2.78	1.124	0.424	2.65
<i>A. tenuis</i>	1.134	0.382	2.96	1.260	0.439	2.87
<i>A. gigantea</i> var. <i>dispar</i>	1.144	0.473	2.41	1.244	0.536	2.32
<i>A. stolonifera</i> var. <i>stolonifera</i>	0.910	0.371	2.45	1.024	0.440	2.32
<i>A. stolonifera</i> var. <i>palustris</i>						

The ratio of the length to the breadth is also tabulated; and it is seen to vary from species to species. This ratio was found to be more constant for different samples of grain of a species than were the actual dimensions. After imbibition the grains are relatively broader in all the species except *A. setacea*, in which the greatest increase is along the longitudinal axis.

Germination tests.

Different samples of seed of the four species *A. stolonifera*, *A. gigantea*, *A. tenuis*, and *A. canina* were tested for percentage of germination. The seeds were sown in petri-dishes on filter-paper kept moist by a cotton-wool wick. Each piece of paper was divided into one hundred squares and a seed placed in each division. Four plates were prepared of each sample of seed, and two were kept in the light and two in the dark. The number of seeds germinated after a given time is shown graphically (figs. 11 *a*, *b*, *c*, *d*) for one sample of seed of each species. Germination began in two to four days and extended over a period of a fortnight to three weeks. Germination appears to begin very slightly earlier in the dark than in the light. The germination is at first rapid, about half the seeds having germinated in the first five or six days after the first signs of imbibition; the rate then falls gradually until no more seeds germinate. The percentage of germination varied between 50 and 90, but no significant difference could be detected between the plates in the light and those in the dark, or between those of the different species.

The seedling.

The process of imbibition passes without a pause into germination. After twenty-four hours the small embryo at the base of the caryopsis begins to bulge outwards, and under favourable conditions the coleorhiza emerges before the end of the second day. It is closely followed by the emergence of the apex of the shoot, and both elongate until the young plant is about equal in length to the grain (fig. 12 *a*, *b*). Up to this stage the direction of growth is practically parallel to the long axis of the grain, no matter what its relation to the horizontal, but now gravitational responses are developed in the mesocotyl and primary root, the former growing vertically upwards and the latter

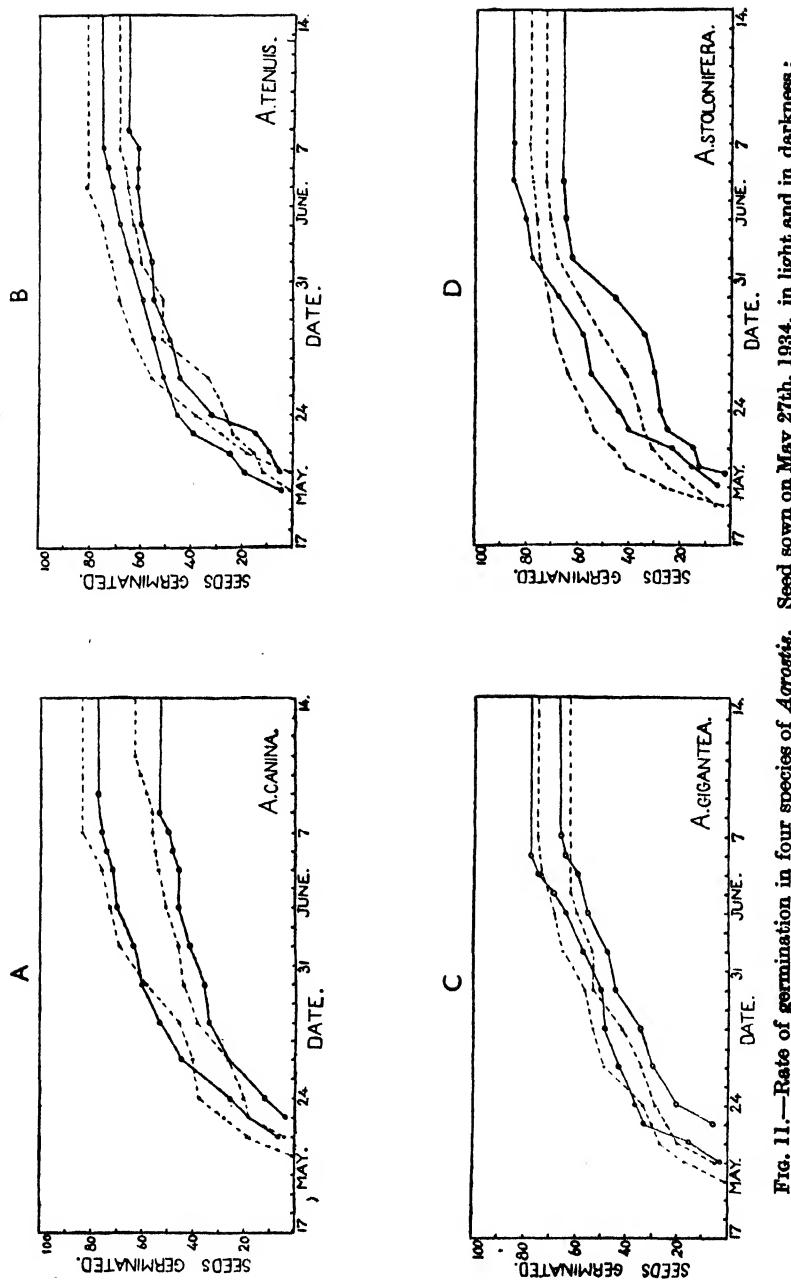


FIG. 11.—Rate of germination in four species of *Agrostis*. Seed sown on May 27th, 1934, in light and in darkness : in light the continuous line, in darkness the interrupted line.

vertically down. The coleorhiza is unaffected by gravity, the primary root bursting its lower side if the grain is lying horizontally and its tip if the grain is vertical. The upward growth of the shoot is due to the mesocotyl, which, in the light, elongates only sufficiently to bring the tip of the coleoptile vertical. Once this position has been attained growth ceases, and the shoot is no longer geotropic, its further growth being influenced only by the direction of the illumination to which the coleoptile is very sensitive. In the dark the mesocotyl elongates indefinitely in an endeavour to bring the coleoptile to the surface and the light; negative geotropism is therefore retained by the shoot in the dark, for the mesocotyl remains sensitive as long as it is actively growing. The primary root always retains its positive geotropism.

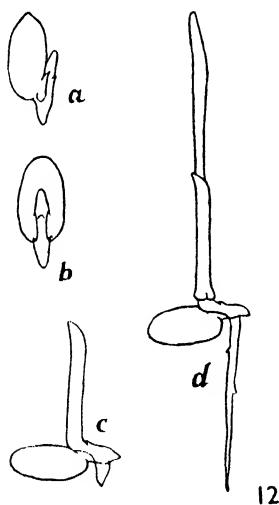


FIG. 12.—Germination of *A. stolonifera*:
a and b, on the second day; c, on
the third, and d, on the fourth after
germination commenced.

FIG. 14.—Development of the panicle of
A. stolonifera. A, B, and C are
successive stages; D is the lowest
branch-system of C.

By the end of the third day after the first emergence of the root the coleoptile is vertical and two to three times the length of the grain (fig. 12 c); the primary root has burst the coleorhiza and may be nearly as long as the grain, though its growth is often arrested on filter-paper. During the fourth day the first leaf bursts the tip of the coleoptile and adventitious roots form as a ring of swellings around the junction of the mesocotyl and the coleoptile (fig. 12 d). In seedlings kept in the dark the leaf never emerges and roots do not form, the entire resources of the grain being spent in the great elongation of the mesocotyl.

The early development of the plant is most easily seen in plants which have been germinated on filter-paper; but, after a few days, development ceases to

be normal under these conditions, so that the further development is described from seedlings sown in soil in pots and which were dug up at intervals and carefully cleaned for examination under the binocular microscope. The development of one plant cannot be traced by this method, but the general scheme of development of the habit of the adult plants can be made out.

At the end of the first week after germination the seedlings have reached the stage shown in fig. 12 d and fig. 13 a, with the first leaf well protruded from the coleoptile and the primary root many times longer than the grain and showing slight indications of the secondary roots. The adventitious roots are just discernible at the base of the mesocotyl. The growth in the second week is chiefly underground, lateral branches of the primary root and the

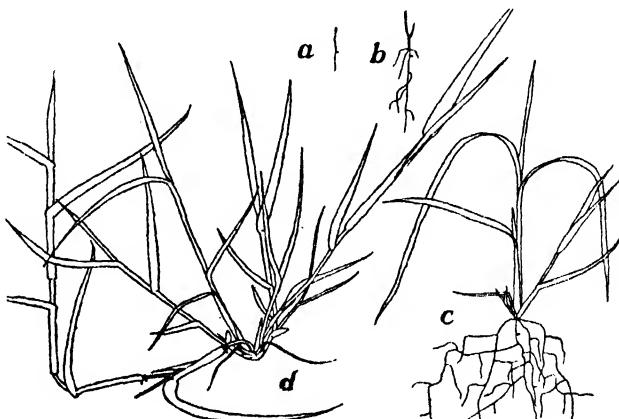


FIG. 13.—Young plants of *A. stolonifera* at successive stages of development :
a, one week ; b, two weeks ; c, three weeks ; and d, six weeks.

adventitious roots becoming long (fig. 13 b) ; the second leaf becomes free from the coleoptile.

During the third week the seedlings begin to develop the habit of the adult plant. Several leaves are produced on the primary axis of the plant, and in the axils of these both intravaginal and extravaginal branches arise (fig. 13 c). The adventitious and primary root-systems are now very complexly branched and extensively developed.

Fig. 13 d shows a plant of *A. stolonifera* six weeks after germination. The main axis of the plant and some of the lateral branches have elongated as stolons and the extravaginal branches have produced leafy shoots without any great production of scale-leaves. Plants of *A. canina* var. *capillaris* at a similar stage show no stolon production, but numerous tufted leafy shoots. The differences in habit of the adult plants are foreshadowed in their seedlings, the ultimate habit depending on the frequency and mode of branching, the degree of elongation of the internodes, the inclination of the leaf-blades, etc., all of which are aspects of the development of the plant.

The two most important differences in habit met with in the British species of this genus—the presence or absence of stolons and rhizomes—are due to the degree of development of the two types of branching, i.e. intravaginal and extravaginal. The simplest habit is seen in *A. setacea*, in which all the branches are intravaginal with short internodes; this is the truly caespitose habit. In *A. canina* the habit may be caespitose with slight extension by underground branches with scale-leaves, as in the variety *arida*, or, as in the variety *fascicularis*, the intravaginal branches may become elongated as stolons, in which case rhizomes are absent. In *A. tenuis* and *A. gigantea* longer or shorter rhizomes are always present and stolons are occasional. In *A. stolonifera* stolons are present and though extravaginal shoots may be numerous they do not extend horizontally below the ground as rhizomes.

Since stolons and rhizomes have a taxonomic importance in the genus, it is necessary to have a clear conception of their morphological differences. Stolons result from the elongation of the internodes of intravaginal branches and bear leaves with well-developed blades to their base; rhizomes, on the other hand, result from the elongation of the extravaginal branches and bear scale-leaves below the ground, and these scales show a transition to vegetative leaves at the surface of the soil. The number of scale-leaves on an extravaginal branch may vary up to an indefinite number, depending on the length of the rhizome, but in *A. stolonifera* and other non-rhizomatous forms, in which the extravaginal shoots ascend at once and are usually produced on aerial branches, there are not more than two or three scale-leaves. Stolons frequently become buried beneath the soil, especially in their second season, but they may always be distinguished from rhizomes by the withered remains of the vegetative leaves. Very rarely stolons may be deeply buried in loose sand while still in a young state, and the extravaginal branches produced in the axils of their leaves may then bear more than three scale-leaves before they reach the surface. These additional scale-leaves can be artificially induced in plants which never bear rhizomes by burying stolons in the soil. This shows that the essential difference between rhizomatous and non-rhizomatous plants is the geotropic response of the extravaginal branches.

The growth of the plant in its early stages is very uniform in all the species. Branches appear in the axils of all the foliage leaves of the main axis, and also in the axils of the prophylls and some of the leaves of the lateral branches. These branches may remain short, but in stoloniferous plants may elongate at once, so that the first leaf is separated from the prophyll by a long internode. The main axis itself may also elongate as a stolon, the first long internode appearing as early as between the second and third leaves.

Extravaginal branches may form in any of the leaf-axils, even those with an intravaginal branch. Often one bursts the sheath of each of the first two leaves, developing at the outside of the fan-shaped young plant. Their prophylls are followed by a scale-leaf and then transitional leaves, the fourth leaf usually having a well-developed blade. In older specimens of rhizomatous plants the extravaginal branches develop horizontally, and continue to bear scale-leaves.

Perenniation.

All the British species of *Agrostis* are perennial, but they do not all survive the winter by quite the same means. The different species and the strains within these species differ in the amount of growth that takes place in the autumn after flowering and also in the earliness of the renewed growth in the spring. In mild winters the stoloniferous forms may never be quite dormant, and the same is true of rhizomes, which may continue to elongate under the ground during the greater part of the winter.

There are three chief means of perenniation in the genus, and that which predominates in any given species depends on the habits of the plants. In a purely caespitose grass like *A. setacea* numerous sterile shoots and flowering culms are produced each spring. The apices of the sterile shoots survive the winter to form panicles the following season and then die. A new crop of sterile shoots forms from buds in the axils of the leaves of the culms and sterile shoots of the previous season. Perenniation is therefore in the form of buds closely invested in leaf-sheaths. Although sterile shoots may be formed at the base of old culms, this process cannot be continued indefinitely, so that old clumps die in the centre.

This means of perenniation is seen in all the species, but it is usually supplemented either by the presence of stolons or rhizomes or both. Stolons are often well protected by the mass of vegetation among which they creep, and in open winters will show an astonishing amount of growth. In the axils of their leaves are buds which may either grow out as leafy shoots in the autumn or may remain dormant until the spring. The shoots at the nodes of stolons may become very much branched in their turn, forming small rosettes at each internode. The rosettes become rooted to the soil and when growth begins in the spring they resemble young plants.

Rhizomes are formed throughout the growing period of the plants on which they are found, and may reach the surface and become aerial leafy shoots in the same season, or their growth may be arrested while they are still spreading horizontally beneath the soil. In the latter case, on the renewal of growth in the spring, they send up sterile shoots from their apices and also as lateral branches from their nodes.

The development of the panicle.

Panicles develop on young plants in their second year, and on older plants they form at the apices of shoots which were formed as sterile innovations the previous season. A short account of the development of the intricate branch system has already been published for the species *A. canina* (Philipson, 1936); in the other species the development is essentially the same.

Immediately after the formation of the rudiment of the uppermost leaf the stem-apex becomes transformed into the panicle primordium. The distichous arrangement of the vegetative leaves is continued upwards as a series of swellings on each side of the axis. These swellings are the bract-primordia in whose

axils the branches of the panicle arise and their distichous arrangement leads to the alternation of the semi-verticils in the mature panicle. These bract-primordia soon encircle the rhachis, giving to it a strongly noded appearance ; usually these bracts do not develop further and cannot be made out in the mature panicle ; but rarely that at the lowest verticil may become enlarged and form a distinct bract.

The primordium of the main branch of each verticil appears as a swelling in the axils of the bract-primordia in a succession from below upwards (fig. 14 A). As was stressed in the case of *A. canina*, although the branches appear in this basifugal order they do not continue to develop to maturity in it. There is a lag in the development of the verticils which is more marked the lower the branch is on the rhachis. The result is that the upper branches increase in size and divide at a very much quicker rate than the lower. Branchlets appear on each main branch in a distichous manner, and the verticils grow as a fan-shaped mass of branches which gradually half-surround the rhachis overlapping the verticils above and on the opposite side of the rhachis (fig. 14 C).

The apex of the rhachis continues growth for some time, giving rise to a regular sequence of branch-primordia in the axils of the minute bracts. Eventually its growth is arrested by the appearance of the rudiments of spikelets at the apex, and the branches immediately below are arrested and remain small for the same reason. It results that, at the stage when all the verticils have been laid down, the largest verticils are a short distance below the apex. The verticils above will always remain relatively small, giving a more or less pointed apex to the mature panicle. The development of the lower verticils may, however, vary in three ways, resulting in the three chief panicle-shapes found among the species. If the verticils continue to enlarge until the lowest has more than compensated for the lag in its development, there will result a downward succession of increasingly larger verticils—that is, the panicle will be pyramidal. If, however, the growth stops when all the verticils (except those at the apex) are equal in size, a cylindrical panicle will result. If the growth is stopped before the lag has been compensated for, the lower verticils will be smaller, giving an ovoid panicle. Reference to the systematic descriptions will show that the shape of the panicle is of some taxonomic importance.

As the branches and the spikelets on their extremities develop, the internodes of the rhachis elongate, until the young panicle completely fills the protective uppermost leaf-sheath of the culm and the upper spikelets protrude. It is evident from the order of appearance that these spikelets will be the most advanced, and indeed those of the lowest verticil may still be very minute. The whole panicle is protruded from the sheath by the end of a fortnight, and the branches expand to a greater or less extent as flowering begins.

The rate of elongation of the panicle and the peduncle in ten plants is shown in Table V. The measurements were made at intervals of a week, and are expressed in millimetres. The earlier development of the panicle as compared

TABLE V.—Rate of elongation of the panicle and peduncle (in mm.).

Species.	Plant.	May 21.	May 28.	June 4.	June 11.	June 18.	June 25.	July 2.	July 9.	July 16.
<i>A. canina</i>	C 5 { Pan. Ped.	7	15	40	83	93	117	—	—	—
	C 7 { Pan. Ped.	—	—	1	3	11	42	72	190	—
<i>A. tenuis</i>	A 4 { Pan. Ped.	11	29	104	150	—	—	—	—	—
	A 25 { Pan. Ped.	—	—	8	12	25	70	150	272	—
<i>A. stolonifera</i> var. <i>stolonifera</i> .	A 5 { Pan. Ped.	4	9	11	86	143	—	—	—	—
	D 5 { Pan. Ped.	—	—	—	2	5	50	130	—	—
<i>A. stolonifera</i> var. <i>stolonifera</i> .	A 14 { Pan. Ped.	1	2	13	72	92	100	—	—	—
	A 16 { Pan. Ped.	—	—	—	2	3	22	85	112	—
<i>A. stolonifera</i> var. <i>palustris</i> . . .	D 6 { Pan. Ped.	1	2	3	8	35	112	—	—	—
	D 7 { Pan. Ped.	0·5	1	1·5	2	8	68	89	100	—

with the peduncle is clearly shown. The development in both is at first slow, gradually becoming very rapid, but the panicle differs from the peduncle in showing a falling off of the growth-rate towards the end. These growth-rates of the panicle and the peduncle are shown graphically for the plant A 16 in fig. 15. Since the panicle elongates at a number of points—that is, at each of the nodes of the rhachis—it will show its most rapid elongation when most of these growing points are active. As more and more of the meristems cease to function the growth-rate of the panicle will fall. It is probable that each individual meristem has the same type of growth-rate as has the peduncle.

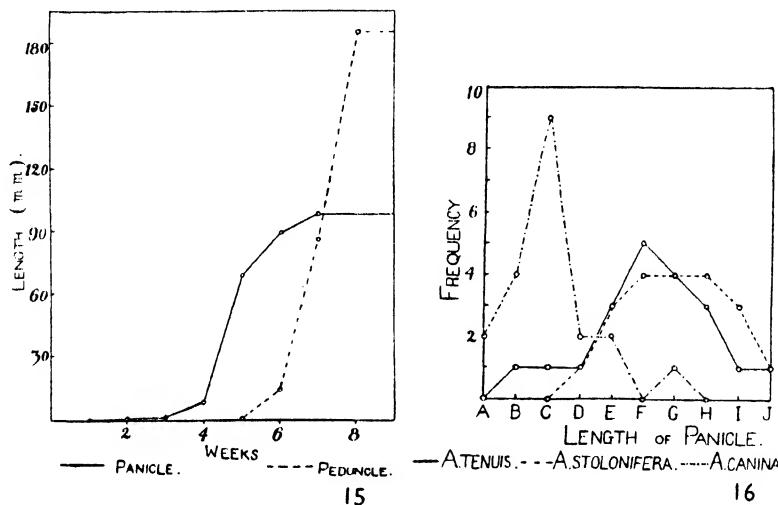


FIG. 15.—The rate of elongation of the panicle and peduncle in a plant (A 16) of *A. stolonifera* var. *stolonifera*.

FIG. 16.—The length of young panicles in 20 plants of each of three species of *Agrostis* on June 17, 1935.

The rapid elongation of the peduncle does not begin until the panicle is nearly completely developed—that is, until the upper spikelets have protruded from the sheath and are nearly ready to flower.

The development of the spikelet.

The development of the individual spikelets has been made the subject of a separate paper (Philipson, 1936). The development was described for *A. canina* as seen both externally and by the aid of serial sections. Three other species (viz. *A. stolonifera*, *A. gigantea*, and *A. tenuis*) were investigated in this way, but, since the development in them all is so very similar, it is proposed only to indicate the few points of difference between the different species.

The tips of the branchlets become spikelet-primordia by the appearance of glume-rudiments, and the lemma, palea, androecium, and gynoecium appear and develop to maturity in that order. Since the characters of the mature lemma and palea are very useful in the diagnosis of the species, it is interesting to follow their development. There are typically five nerves in the lemma, which are laid down in the order—mid-rib, two laterals, and two marginals. In *A. tenuis*, in which there are only three distinct nerves in the lemma, it is not the marginal nerves which are absent but the laterals, and in the other species the laterals are not so strongly developed nor do they run so high into the lemma as do the marginal nerves, although the latter are developed last.

The presence or absence of the awn is of very dubious systematic value. It may be present in all the British species except *A. semiverticillata* and may also be absent in all the species except perhaps *A. setacea*. The awn-rudiment is formed by a division of the apex of the lemma tangential to the floral axis. The awn cannot be considered as an epidermal outgrowth, as it may receive the mid-rib, nor can it be the true apex of the blade-region of the lemma, as this is also represented in the apex of the lamina of the lemma. The awn must be considered as a dorsal outgrowth belonging to none of the classical morphological categories. In the section on 'Variation' the variation in awn-length in plants of *A. canina* is tabulated. It is difficult to understand what factors influence the appearance of an awn in some spikelets of a panicle and not in others. When the awn is present the back of the lemma is curved to accommodate it, and on each side of this curve the lemma is thickened, and it is here that the lateral nerves run. In spikelets of *A. tenuis* which are awned these thickened lines are present on each side of the awn, and it is interesting that the lateral nerves run in them as in the other awned species, while in unawned spikelets of *A. tenuis* the lateral nerves are absent.

The palea is enclosed by the lemma and occupies the space across the two anterior stamen-rudiments. In the early stages of its growth it is similar in all the species—that is, the minute size found in *A. canina* is not foreshadowed at its inception. As the stamen-filaments increase in length the palea keeps pace, but the growth is soon arrested in *A. canina*, so that it remains minute in the adult spikelet.

Flowering.

The earliest rudiments of the panicles can be found early in May, and rather more than a month later the panicles begin to protrude from the leaf-sheaths. From the protrusion of the first spikelet to the first flowering occupies on an average another fourteen days. The different plants of a given species come into flower over a considerable range of time, but it is possible to detect that some species come into flower and reach the maximum flowering-period earlier than others.

In order to obtain a clear conception of the relative flowering-periods of the three species *A. canina*, *A. tenuis*, and *A. stolonifera*, the length of the young

panicles was scored in twenty plants (all of the type-varieties) of each of these species growing in the Experimental Plots at Kew. The panicle-length relative to the uppermost leaf-sheath was divided into ten easily scored categories, listed below, which are used as abscissæ in the diagram (fig. 16), and the frequencies of these categories in the twenty plants are used as ordinates :—

The characters used in the scoring of panicle-length.

A. Fully protruded.	F. Just included in the sheath.
B. More than $\frac{1}{2}$ protruded.	G. More than $\frac{1}{2}$ length of the sheath.
C. $\frac{1}{2}$ protruded.	H. $\frac{1}{2}$ length of the sheath.
D. Less than $\frac{1}{2}$ protruded.	I. Less than $\frac{1}{2}$ the length of the sheath.
E. Just protruded.	J. Very young.

These categories give a better comparison between the different plants and different species, in which the panicles are of different sizes in the mature state,

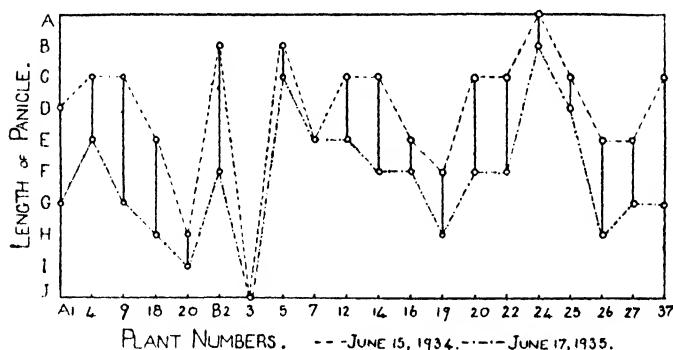


FIG. 17.—Diagram to show the correlation between the length of the panicle in 20 plants of *A. tenuis* in two seasons.

than would actual measurements. The degree of protrusion of the panicle is clearly proportionate to the earliness of flowering, and *A. canina* is clearly the earliest species to flower. Moreover, since this species shows a well-defined mode, its period of flowering will probably be short. *A. stolonifera* is slightly later to flower than *A. tenuis*, and both these species have ill-defined modes, indicating that the period of maximum flowering will be protracted.

The different plants of a species come into flower on different dates. From the data which were collected over two flowering seasons (1934–35) it is evident that the relative time of flowering remains more or less constant for a given plant. This is shown clearly for *A. tenuis* in fig. 17 which is a diagram to show the correlation between the panicle-length of individual plants on corresponding days of two seasons. The lengths of the panicles were scored by means of the same ten categories and the heavy vertical lines connect the lengths of each

panicle in the two seasons ; the two broken lines connect the panicle-lengths each of one season. It can be seen that there is a fairly constant difference between the two seasons, the panicles being more (or rarely equally) advanced in 1934, and that the same plants were early to flower in one season as in the next.

The time of flowering is also dependent to some extent on the degree of latitude. For example, in the low-lying parts of Westmorland in the summer of 1933 the first plants of *A. tenuis* did not come into flower until the last week of June, whereas in Cambridgeshire plants were flowering at least a week earlier. Altitude also affects the time of flowering, for in Cardigan in 1934 *A. canina* growing almost at sea-level in Borth Bog had all the panicles with open spikelets on the basal branches on July 3rd, but on the slopes of Drybedd at from 1200–1400 ft. (370–430 metres) two days later most of the panicles

TABLE VI.—Times of anthesis.

Species.	Godron *.	Splechtner *.	Fruwirth *.	Wright †.	Philipson †.
<i>A. stolonifera</i>	11.0 a.m.	—	12.0 a.m.	—	10.0 – 11.30 a.m.
<i>A. gigantea</i>	—	6.30–7.30 a.m.	—	4.0– 4.30 p.m.	2.30– 3.30 a.m.
<i>A. tenuis</i>	11.0 a.m.	—	—	4.0– 4.30 p.m.	1.0 – 2.30 p.m.
<i>A. canina</i>	11.0 a.m.	—	—	5.0– 6.30 a.m.	4.0 – 5.0 a.m.
<i>A. setacea</i>	—	—	—	—	4.30– 5.30 a.m.

were not protruded, and were a week or more behind those at sea-level. Similar differences have been noted in South Wales, the Lake District, and Northumberland.

The process of flowering in a given plant takes place during a limited period each day. The different plants of a species have been found to flower at much the same time at Kew, and the species each have a distinct time at which anthesis is at a maximum. The results of other workers are tabulated (Table VI), and the discrepancies may be due to the alteration of flowering time by external conditions or to the uncertainty of taxonomy and nomenclature which is so frequent in this genus.

The time of flowering certainly varies with the conditions of weather and station ; but it has not been possible to analyse these effects in detail. The good

* See Bibliography (p. 150).

† Times are Greenwich Mean Time.

agreement between the results at Kew and those obtained by Wright at Bingley (who has kindly permitted me to use his unpublished data) show that the time of flowering is probably constant in a species within very narrow limits. The results obtained at Kew were all taken in the Experimental Plots with plants of very diverse origin. It is significant that on June 27, 1935, twelve plants of *A. canina* (that is, all that were in flower) began to shed their pollen within fifteen minutes of each other, though the plants belonged to different varieties and had been brought from Scotland, Ireland, Wales, and various parts of England.

Flowering in a given spikelet is begun by the anthers swelling and becoming prominently visible through the glumes. When the time of flowering arrives the glumes open slightly at first, probably merely by the slight protrusion of the anthers, but after a longer or shorter period of rest in this position, perhaps of minutes only or even hours, the gape of 10° - 20° is quickly changed to one

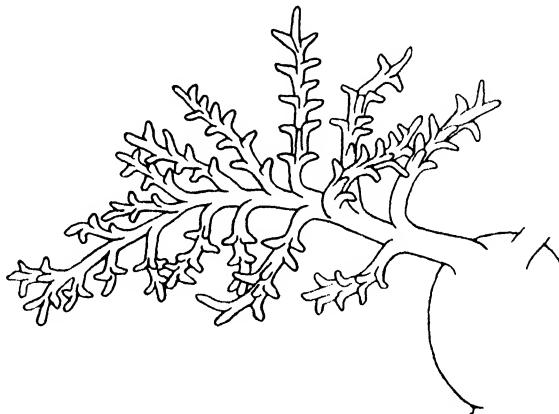


FIG. 18.—Stigma of *A. canina*.

of about 50° , and if a spikelet is dissected in this condition the swollen lodicules will be seen between the ovary and the lemma. During the few minutes required for this swelling of the lodicules the filaments elongate and the anthers protrude above the lemma. Dehiscence begins at the apex of each lobe and can be seen to move quickly to the base. The anthers usually become pendulous; but on a still day they may remain jammed between the apices of the glumes. The pollen may be dispersed gently or in a sudden cloud if the plant is jolted. During dehiscence the stigmas bend slowly outwards, and about fifteen minutes after the swelling of the lodicules they are spread horizontally from the angle between the gaping glumes.

The diameter of fresh pollen was measured (Table VII) and the species have different but not distinct ranges of pollen-size. The stigmas are inserted below the apex of the ovary and are simply plumose (fig. 18) with papillose cells on the branches.

The closing of the spikelet is a more variable process than the opening. The glumes may close again shortly after dehiscence trapping the empty anthers or they may close more slowly when usually the anthers break off. Spikelets frequently open again on the second day when if the anthers are still present they may be confused with flowering spikelets, and since these spikelets are the first to open a mistaken flowering-time may be recorded. It was thought at first that these spikelets might have remained unpollinated on the first day, but since the stigmas were never seen exserted on the second day this does not seem probable. The glumes may remain gaping until the evening of the day of flowering, that is in *A. canina* for over twelve hours, and during all this time the stigmas may not be withdrawn but remain horizontal. It is usual, however, for the stigmas to become vertical within an hour of flowering and for the glumes to close.

Flowering in a panicle begins at the apex, and on the first day usually very few spikelets at the apices of the uppermost branches open, but on the second day the whole of the upper half or two-thirds of the panicle will be in flower,

TABLE VII.—Pollen-size.

<i>A. setacea</i>	1·8–2·8 μ	<i>A. gigantea</i>	3·4–4·6 μ
<i>A. canina</i>	1·8–2·8 μ	<i>A. stolonifera</i>	3·4–4·6 μ
<i>A. tenuis</i>	2·4–3·4 μ	<i>A. semiverticillata</i> ...	2·4–3·4 μ

and on the third day spikelets on the basal branches will open so that the whole panicle flowers in from three to five days.

The period over which anthesis takes place on a given day varies in the different species; but each has a clearly marked maximum period. In *A. canina* flowering is soon over, and all the plants flowered at much the same time. In *A. tenuis*, on the other hand, flowering began more gradually, the maximum period being perhaps an hour after the first spikelets opened and the different plants did not flower so simultaneously. *A. stolonifera* and *A. gigantea* resembled *A. tenuis* in this respect.

In *A. canina* there was a tendency, especially on the later days of flowering, for the branchlets to close against the branches and for these to be raised slightly during the morning and late afternoon, to spread again before flowering the next morning. In *A. stolonifera* this closing was not so noticeable, but the panicles of both these species and of *A. setacea* become tightly closed and spike-like immediately after the panicle has finished flowering. Plants of both *A. canina* and *A. stolonifera* were observed to be flowering at the apex of the panicle before it had begun to expand, and rarely the panicle would remain spike-like throughout the flowering period. The panicles of *A. tenuis* and *A. gigantea* remain spreading after flowering, although the branchlets may close against the branches, especially in the latter species.

All the panicles of a plant do not begin to flower on the same day, but the last to flower is seldom more than two or three days after the first. The difference between different plants of the same species is more considerable, not only because of differences in their environment but because of an inherent difference which has already been shown to be constant in a plant from year to year. Similarly there is little or no appreciable difference between the time of day at which panicles of the same plant begin to flower, but there may be a difference of an hour or more between different plants of the same species.

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SUMMARY.

1. A taxonomic revision of the British species of *Agrostis* has been made and the forms arranged under the following species and varieties, to which a Key is given :—

1. *Agrostis setacea* Curtis.
2. —— *canina* (Linn.) var. *fascicularis* Sinclair.
3. —— —— var. *arida* Schlecht.
4. —— *tenuis* (Sibth.) var. *hispida* (Willd.) Philipson.
5. —— —— var. *humilis* (Aschers. & Graebn.) Druce.
6. —— *gigantea* (Roth) var. *ramosa* (S. F. Gray) Philipson.
7. —— —— var. *dispar* (Michx.) Philipson.
8. —— *stolonifera* (Linn.) var. *stolonifera* (Linn.) Koch.
9. —— —— var. *palustris* (Huds.) Farw.
10. —— *semiverticillata* (Forssk.) Christens.

Each of these species and varieties are described and a complete synonymy is given. Representative specimens from several British herbaria are cited and notes on distribution, flowering, etc., are included. Variations of less than varietal rank are recorded, and in the case of *A. stolonifera* var. *stolonifera* four ecads are recognized.

One inter-generic and two inter-specific hybrids are described.

Short diagnoses are given of the alien species, and a Key to all the species, native and alien, is provided.

2. The phenomena of variation and fluctuation are examined as they occur within the species and in natural populations, and upon this data a discussion of the status of the taxonomic categories is based.

3. The anatomy of the species and more important varieties is described, and its relationship to taxonomy is discussed.

4. The development of the plants from germination to flowering is described, especial emphasis being given to those characters which are of taxonomic importance.

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AGROSTIS SETACEA CURT.



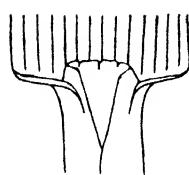
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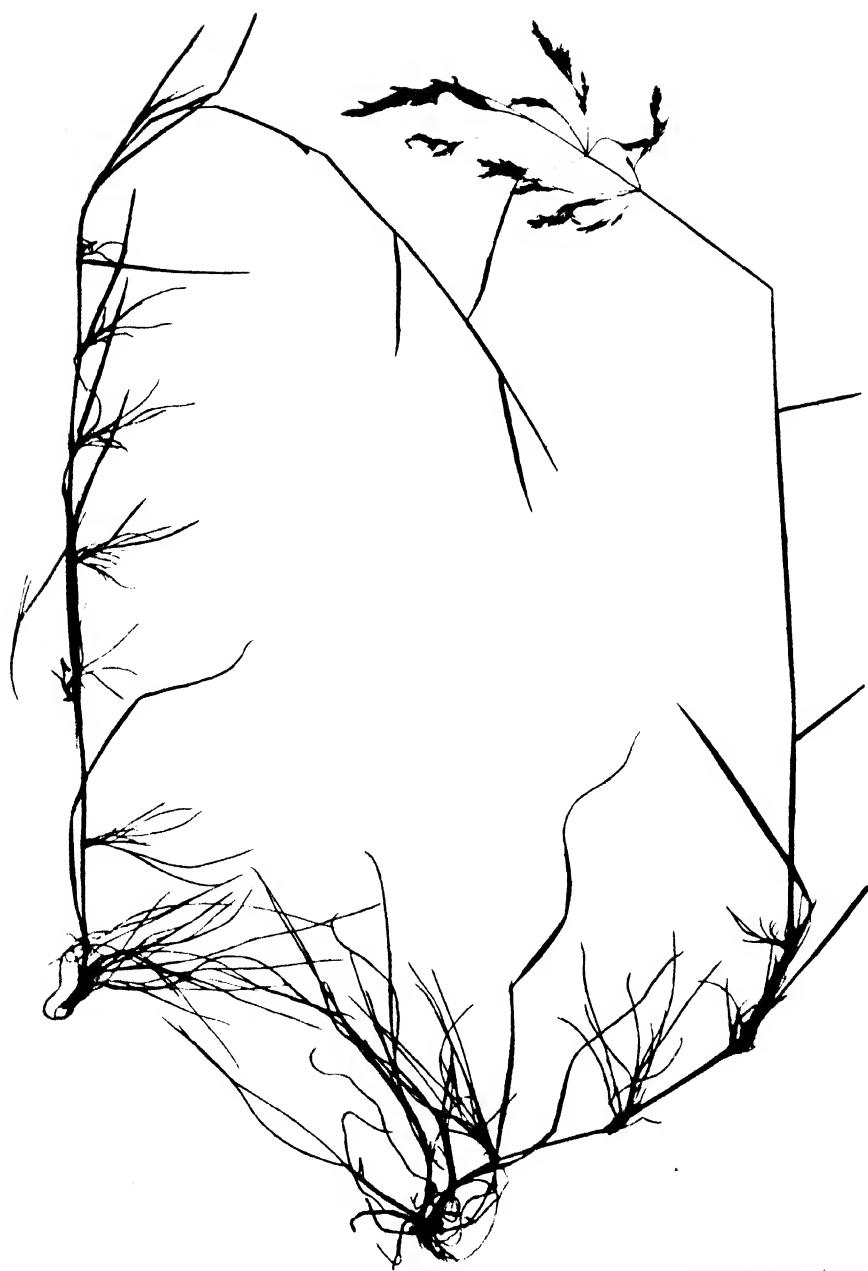
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AGROSTIS STOLONIFERA VAR. PALUSTRIS (HUDS.) FARW.



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EXPLANATION OF THE PLATES.

PLATE 4.—*A. setacea* Curtis. Inset: above, ligule; below, spikelet, lemma, ovary with palea and lodicule.

PLATE 5.—*A. canina* var. *fascicularis* (Curtis) Sinclair.

PLATE 6.—*A. canina* var. *arida* Schlecht. Inset: left, ligule; right, spikelet, lemma, ovary with palea and lodicule.

PLATE 7.—*A. tenuis* var. *hispida* (Willd.) Philipson. Inset: left, spikelet, lemma, palea, lodicules (above); right, ligule.

PLATE 8.—*A. tenuis* var. *humilis* (Aschers. & Graebn.) Druce.

PLATE 9.—*A. gigantea* var. *ramosa* (S. F. Gray) Philipson.

PLATE 10.—*A. gigantea* var. *dixpar* (Michx.) Philipson. Inset: above, ligule; below, spikelet, lemma, palea, lodicules (above).

PLATE 11.—*A. stolonifera* var. *stolonifera* ecas *stolonifera* (Linn.) Philipson. Inset: spikelet, lemma, palea, lodicules (above), ligule.

PLATE 12.—*A. stolonifera* var. *stolonifera* ecas *calcicola* Philipson. Type specimen.

PLATE 13.—*A. stolonifera* var. *palustris* (Huds.) Farw.

PLATE 14.—*A. canina* var. *fascicularis* Sinclair. Collected in a marsh in shade, at Sweet-hope Lough, Northumberland.

PLATE 15.—*A. canina* var. *fascicularis* Sinclair. From the same plant as Plate 14, after cultivation at Kew.

PLATE 16.—*A. tenuis* Sibth. Collected on dry soil in shade at Box Hill, Surrey.

PLATE 17.—*A. tenuis* Sibth. From the same plant as Plate 16, after cultivation at Kew.

PLATE 18.—*A. stolonifera* var. *palustris* (Huds.) Farw. Box Hill, Surrey, growing with the plant in Plate 19.

PLATE 19.—*A. gigantea* var. *ramosa* (Gray) Philipson. Box Hill, Surrey, growing with the plant in Plate 18.

PLATE 20.—*A. stolonifera* var. *stolonifera* (Linn.) Koch. Borth, Cardigan, growing with the plant in Plate 21.

PLATE 21.—*A. tenuis* Sibth. Borth, Cardigan, growing with the plant in Plate 20.

A taxonomic study of the genus *Lavandula*. By Miss D. A. CHAYTOR (afterwards Mrs. MANLEY). (Communicated by Sir ARTHUR W. HILL, K.C.M.G., F.R.S., F.L.S.)

(With 39 figures in the text)

[Read 28 October 1937]

THE genus *Lavandula* is well known on account of the economic and horticultural value of certain of its species. It is also of considerable botanical interest, and a number of problems arise when the species are studied comparatively. The present paper deals with these problems and with the more strictly botanical aspects of the genus. Such a survey is essential for the proper study of the cultivated lavenders, which it is hoped to consider at a later date when further experimental work has been completed.

The literature on the genus is very extensive, since species of *Lavandula* have been known and discussed by botanical writers from very early times. Certain species were known to the ancient Greeks and also to Latin writers. The later mediaeval and pre-Linnaean literature contains many references to *Lavandula*; but as these, especially such as occur in the Herbals, mostly refer to cultivated forms and their supposed virtues, they are not dealt with in this paper.

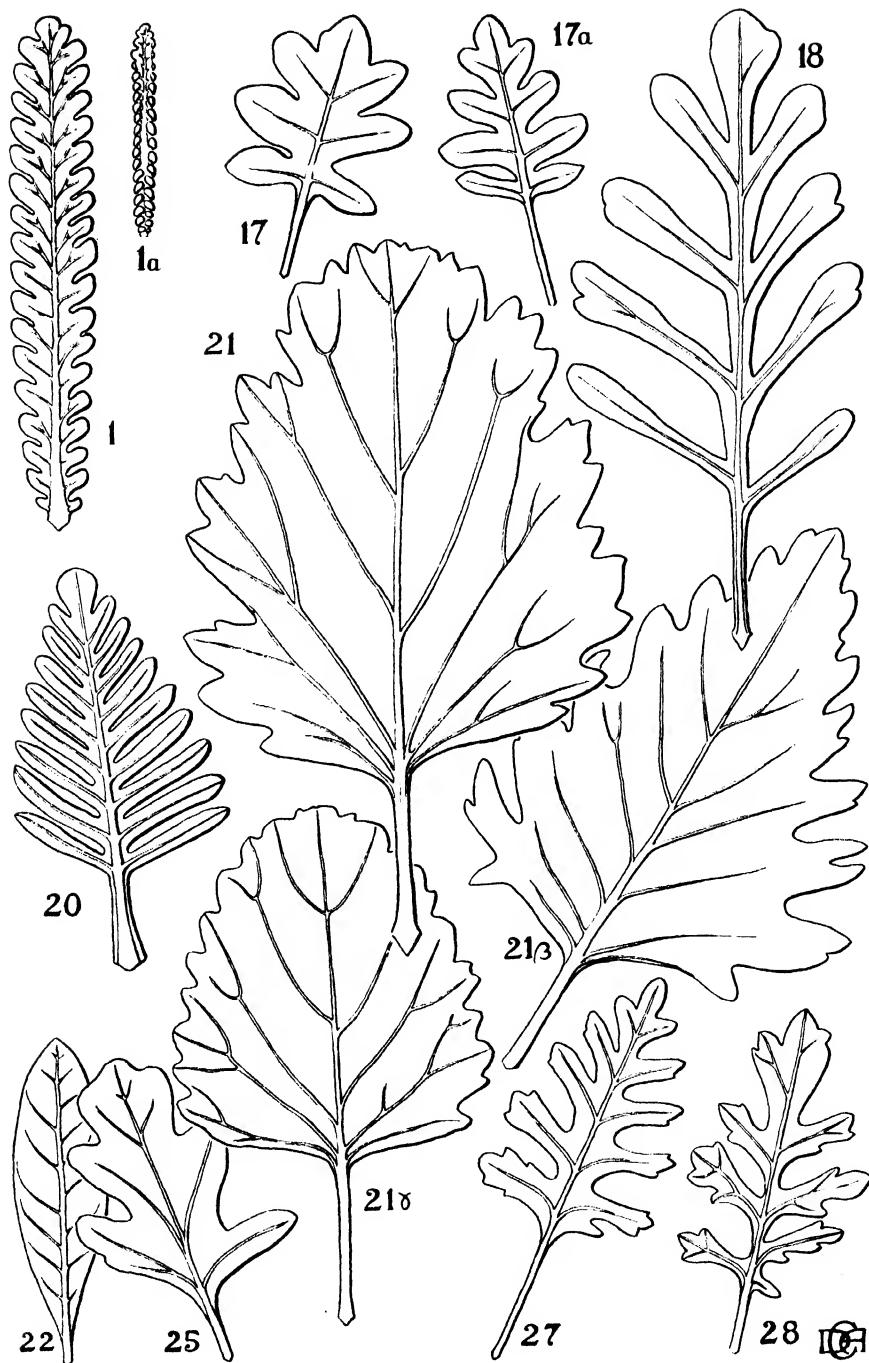
In the 'Species Plantarum' (1753) Linné mentions four species. Two monographs dealing exclusively with the genus *Lavandula* were subsequently published: the earlier, in 1780, by the younger Linné ('De Lavandula'), and the later, in 1826, by Baron F. C. J. de Gingins de Lassaraz ('Histoire Naturelle des Lavandes'). The first of these was a short work which has been almost entirely superseded by more modern publications; but Gingins de Lassaraz's treatise is still of great value. He deals accurately and at length with the previous history of the genus and with the geographical distribution, properties, uses, and classification. The species known to him numbered 12. Bentham, in his monograph of the Labiatae (1833) and in de Candolle's 'Prodromus' (1848), gives full descriptions of the genus and species, 18 species being accepted by him in the 'Prodromus'. New species and varieties have subsequently been found and described; and the genus has been discussed by numerous authors in Floras, works on systematic botany, and papers in periodicals. These species and varieties have been studied, often with the aid of original specimens, and their status is discussed in the present paper. It has been necessary to make several reductions. In all 28 species are

recognized, excluding hybrids. One species, *L. somaliensis* Chaytor, received from British Somaliland, is described for the first time.

The classification used in this paper is based upon those of Gingins de Lassaraz (op. cit. pp. 119, 128) and Bentham ('Labiatae', I, p. 151 and in DC. Prodr. XII, p. 143). The genus is divided into five sections: the first three were originally constituted and described by Gingins de Lassaraz, the fourth by Bentham, and the last is new. These sections are distinguished by differences of habit, leaf-shape, arrangement of flowers in the spikes and verticils, and by bract- and calyx-characters. The species within each section differ chiefly in small but usually very constant characters of indumentum, bract, and calyx, but also to some extent in habit, leaf-shape, length of peduncle, spikes, flowers, and nucles. The species are by no means always clearly defined, and intermediates which cannot be accounted for by simple hybridization often occur, linking up otherwise distinct species. Such intermediates have often been described as species, and in attempting to determine their true status, whether as full species, subspecies, or varieties, the question of the definition of 'species' as found in the genus *Lavandula* has had to be considered. A similar problem of status also arose when considering the case of slightly differing forms which occur in widely separated geographical areas.

The geographical distribution of the genus is confined to the north temperate and tropical regions of the Old World. Species of *Lavandula* are found in the Atlantic Islands, in the countries surrounding the Mediterranean Basin, in tropical Africa north of latitude 10° N. (including Cape Verde Islands), in Arabia, and in the Indian Peninsula. The distribution of the species provides problems as to their origin. When the distributions of nearly-related groups of species are mapped out, several interesting questions arise. A certain area often appears to serve as a centre of differentiation and distribution of some group of species, though the reason for this is not obvious. It may be that the ecological conditions favour variation, or the accidental contiguity of closely-allied species may permit of hybridization and resulting segregation of allied forms. Examples of such centres occur in the section *Stoechas*, where southern Portugal seems to be the centre of differentiation, and in section *Pterostoechas*, where Algeria-Morocco appears as a region of great instability.

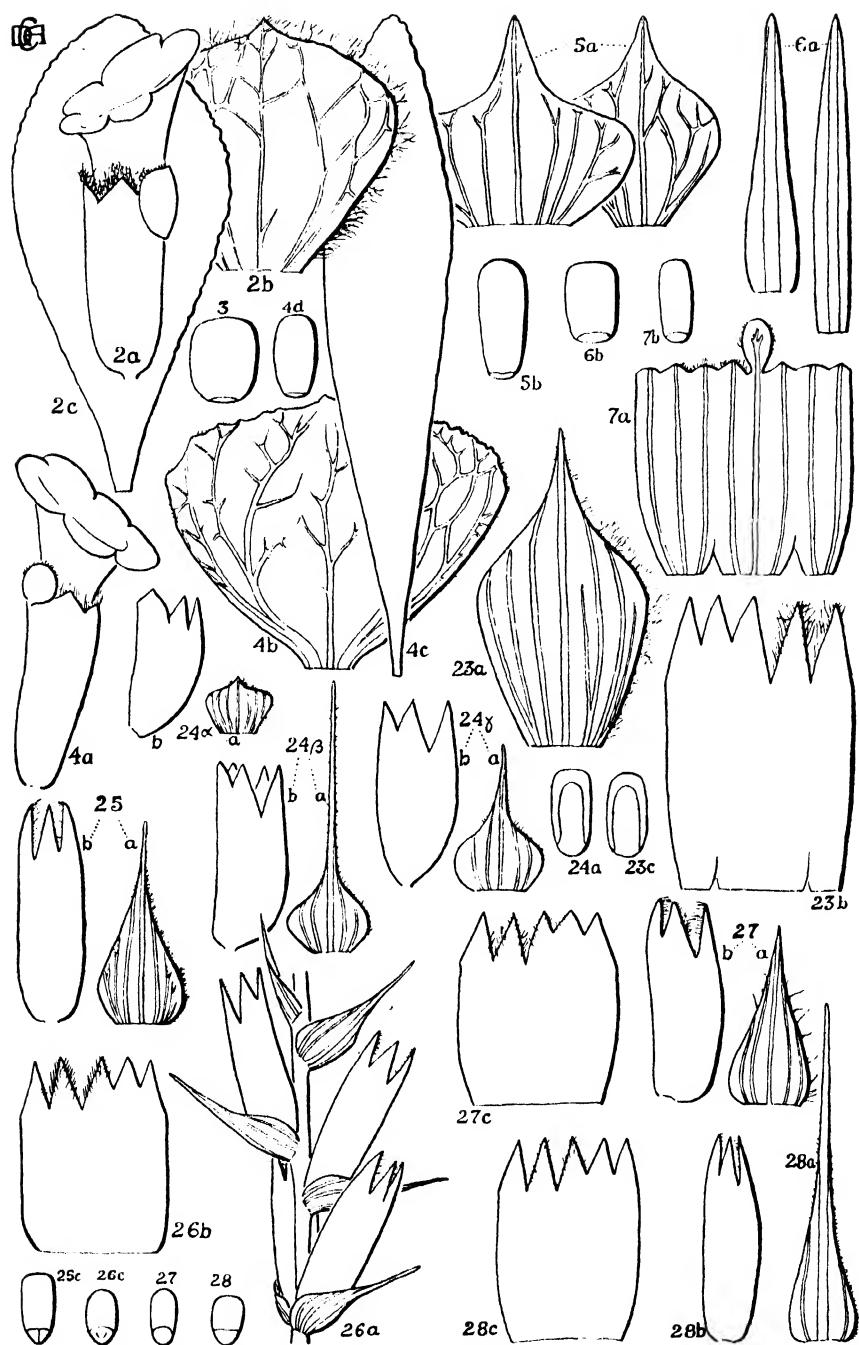
There is no doubt that hybridization occurs between species of *Lavandula* both when wild and in cultivation. Such hybridization is commonest between species of the same section, but is sometimes inter-sectional. In the absence of exact experimental data, such hybrids can only be detected by their morphological characters when these are compared with those of their putative parents. That morphologically different plants may have had the same species as their immediate or original parents is to be explained by the intra-specific variation of several of the more widespread species and by the probable occurrence of segregation and back-crossing. Thus, three apparently distinct hybrid-forms are described (p. 169) with the ancestry *L. Stoechas* × *L. pedunculata*.

Leaves of species nos. 1, 17, 18, etc. $\times 2$.

The work for this paper has been carried out at Kew with constant reference to the Herbarium and Library. My thanks are due to the Director and to the Keeper of the Herbarium for allowing me facilities for this study; also to Dr. W. B. Turrill for his valuable help and advice, and to Mr. G. Atkinson for his assistance with the drawings. Material has been obtained on loan from the Herbarium of the Museum of Paris, from the Geneva Botanic Garden, and from the University of Algeria. Dr. René Maire generously presented a valuable set of specimens of North African species of *Lavandula* to Kew for the purpose of this study. The specimens quoted in the discussions of the various species are intended to be a representative selection for comparative purposes, not a complete list of the specimens studied.

GENERAL DESCRIPTION OF THE GENUS LAVANDULA.

Perennial aromatic herbs or bushes, erect or ascending, the *stems* bushy, much branched and woody, or herbaceous, erect, \pm branched but not bushy. *Root-system* composed of one or a few thick woody main roots, with numerous fibrous branches. Young *stems* rectangular or terete, sometimes ribbed; the basal parts of the bushy species often become very woody and much thickened. *Leaves* simple, entire, dentate, pinnate or bipinnate. *Indumentum* composed of simple, branched or stellate hairs, often with numerous sessile or pedicellate glands. *Inflorescence* a terminal spike borne on a distinct peduncle, which may be simple or branched: spike interrupted, lax or compact, simple or branched at the base, its shape depending upon the arrangement of the bracts, which may be paired, alternate or spiral, imbricate or arranged in vertical tiers: the spike may, then, be cylindrical or 8-, 4-, or 2-seriate. *Bracts* membranaceous or sometimes green or purplish or white, in size and shape supplying critical characters in the diagnosis of several species: they may be all fertile, with 1-7 flowers in the axil of each, or the uppermost may be enlarged, sterile, often coloured, forming a coma or plume (species of section *Stoechas*). *Bracteoles* present only in the species of section *Spica*. *Calyx* sessile or shortly pedicellate, cylindrical or urceolate, often enlarged at fruiting stage, persistent, 5-dentate, the posterior tooth sometimes (species of sections *Stoechas* and *Spica*) enlarged appendiculate, 8-, 13-, or 15-nerved. *Corolla* usually purple or blue, sometimes white or coppery-pink; corolla-tube long, little or much exceeding calyx in length, \pm dilated at the throat; lobes 5, almost uniform or bilabiate 2/3, the posterior pair usually the larger, upright, the anterior three \pm horizontal or reflexed. *Stamens* 4, included in the corolla-tube and inserted on it, the anterior pair longer than the posterior; anther reniform. *Stigma* \pm rotund, of two flattened lobes, appressed except at the receptive stage: style about the length of the corolla-tube. *Nucules* 4, elliptic, oblong or rotund-oblong, attached by the lower outer surface to the 4 lobes of the disk, the mature nucule with a white areole marking this attachment: the nucule-coat smooth or \pm roughened, sometimes with a gelatinous envelope when soaked in water.



KEY TO THE SECTIONS

Verticils many-flowered, up to 7 flowers in the axil of each bract.

Bracteoles sometimes present. Posterior calyx-tooth enlarged into a ± rotund to lanceolate appendage : calyx 8- or 13-nerved, usually shortly pedicellate.

Bracts dimorphic, the uppermost enlarged, coloured or white, sterile. Bracteoles absent. Calyx sessile or pedicellate. Corolla-tube only slightly longer than the calyx : corolla-lobes 5, sub-equal, scarcely bilabiate. Nucules sometimes with a gelatinous coat when wet

Bracts ± uniform, all fertile. Bracteoles present. Calyx shortly pedicellate. Corolla-tube nearly double the calyx-length : corolla-lobes 5, bilabiate, the 2 posterior lobes much the larger. Nucules without a gelatinous coat when wet

Verticils 1- or 2-flowered, 1 flower in the axil of each bract.

Bracteoles absent. Posterior calyx-tooth not appendiculate, though often broader than the others : calyx 15-nerved, sessile.

Bracts arranged in exactly opposite pairs

Bracts alternately or ± spirally arranged.

Areoles $\frac{1}{2}$ length of nucule or more : herbaceous

Areoles $\frac{1}{2}$ to $\frac{1}{3}$ the length of the nucule : scrubby bushes

I. STOECHAS.

II. SPICA.

III. PTEROSTOECHAS.

IV. CHAETOSTACHYS.

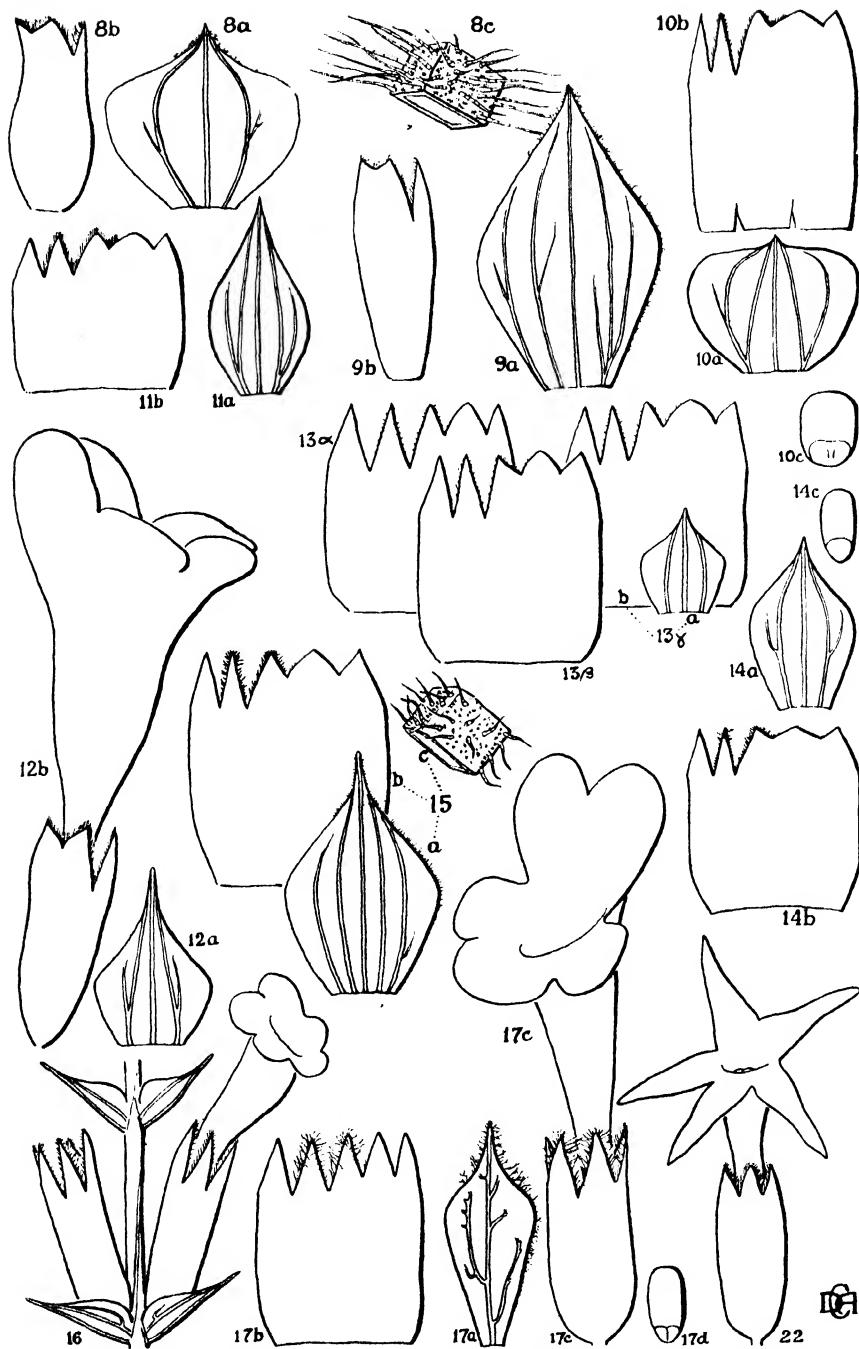
V. SUBNUDA.

SECTION I. STOECHAS Ging. Hist. Nat. Lav. pp. 119, 128 (1826) ;
Benth. Lab. I. p. 147 (1833).

Original diagnosis. Ging. op. cit. p. 128. ‘Charact. Calyx appendiculatus. Flores spicati, bracteis multifloris, floribus ebracteolatis, spica comosa.

Observ. Caryopsides subtriangulares, saepius impunctatae, areola umbilicali minuta ; (ob squamas gynobasi vix adhaerentes). Tubus corollae calycem paulo superans ; (stamina saepius sub-exserta). Arbusculae.’

The habit of species of the section *Stoechas* is bushy, the plants growing to about 1 m. in height, the old stems woody, their bark peeling off in flakes and strips. The leaves are linear, elliptic, lanceolate or oblanceolate, entire, except in one species (*L. dentata*) where they are pectinate-dentate or pinnate-dentate. The peduncles are distinct, unbranched, 1-32 cm. long. The spike is unbranched, oblong, compact (very occasionally interrupted), quadrate or imbricate-cylindrical. The indumentum of the whole plant is usually composed of short white branching hairs, or sometimes of simple hairs, or of both. The young stems, peduncles and leaves are often densely white tomentose or almost lanuginous, the indumentum becoming more sparse with age. The bracts are large, reniform, rotund or ovate, arranged in opposite pairs forming 4 (or 8) vertical rows or ± imbricate, each supporting a contracted cyme of 2-7 flowers ; the uppermost bracts of each spike are usually sterile, enlarged, coloured or white, forming a coma ; transition-stages between normal bracts and coma-bracts are frequent. The section *Stoechas* is unique in the genus in the possession of comae. Bracteoles are absent. The calyx is sessile or shortly pedicellate, 13-nerved, 5-lobed ; the anterior 4 teeth are simple or

Bracts, calyces, nucules, and indumentum of species nos. 8, 9, 10, etc. $\times 6$.

tricuspidate ; the median posterior tooth is enlarged, appendiculate, rotund or reniform, membranous, covering the mouth of the calyx in bud and young fruit, upright at flowering stage and maturity. The corolla-tube slightly, up to 2 mm., longer than the calyx ; its lobes 5, sub-equal. The nucules are rotund-oblong to narrowly oblong, sometimes with a gelatinous envelope when soaked in water ; areole white, minute, transversely elliptic.

KEY TO THE SPECIES OF THE SECTION STOECHAS.

- Leaves dentate or pinnate-dentate 1. *L. dentata*.
- Leaves entire.
 - Peduncles short, 1-2 cm. up to 3.5 cm. Sterile bracts ± broadly obovate or spatulate. Calyx ovate at flowering period 2. *L. Stoechas*.
 - Peduncles medium or long, 3.5-32 cm. Sterile bracts lanceolate, narrowly elliptic, or oblanceolate. Calyx tubular at flowering period.
 - Indumentum of leaves green, short, stiff, ± densely hirsute. Inflorescence white or greenish white ; peduncles 5-7.5 cm. Nucules oblong-rotund 3. *L. viridis*.
 - Indumentum of leaves short, grey, tomentose to pubescent. Inflorescence typically purple, occasionally albino ; peduncles up to 32 cm. Nucules oblong 4. *L. pedunculata*.

Hybrids are recorded of parents within the section, and also, in the cases of *L. dentata* and *L. pedunculata*, with species of section *Spica*.

DISCUSSION OF SECTION STOECHAS.

The species of the section *Stoechas* fall naturally into two groups, *L. dentata* alone in one, *L. viridis*, *L. Stoechas*, and *L. pedunculata* in the other. *L. dentata* is quite distinct from the other three species, striking points of difference being the dentate leaves, lax spike, and short coma composed of ovate-lanceolate sterile bracts. The other three species are very closely allied to one another, and, though typical examples differ in numerous minor points, intermediate types are frequent, especially at the Western limits of the distribution. The most obvious differences in herbarium-material lie in the peduncle length—short in *L. Stoechas*, medium in *L. viridis*, and long in *L. pedunculata* ; this character fails at once for diagnostic purposes, as, apart from normal variation on individual plants, the Portuguese, Atlantic Islands, and NW. African forms of *L. pedunculata* have a peduncle of only medium length. *L. pedunculata* and *L. Stoechas* can, however, be roughly distinguished by the peduncle length, but more critically by certain inflorescence characters (i.e. bract and coma-shape, calyx-shape, length of corolla-tube relative to calyx, and nucule-shape) and to some extent they differ also in leaf-shape. The inflorescence characters of *L. viridis* are more or less intermediate between *L. pedunculata* and *L. Stoechas* ; the leaves are usually larger and broader than in both these species and almost uniform, with only a few that are linear fastigiate ; the main differences, however, lie in the indumentum and in the inflorescence coloration. The indumentum

of the whole plant is \pm densely hirsute, green, not grey-tomentose (except sometimes on the young stems), and the spike—bracts, coma, and corollas—is white or greenish white, not purple or black-purple as in *L. pedunculata* and *L. Stoechas*. Unfortunately, these characters are much more striking in living material than in dried specimens, and the occurrence of albino forms of *L. pedunculata* and *L. Stoechas* makes further difficulties.

The geographical distribution of the three species—*L. pedunculata*, *L. viridis*, and *L. Stoechas*—is interesting. *L. Stoechas* is the most widely distributed and is found in almost the whole of the SW., W., N., and E. Mediterranean regions. With the exception of the Azores, from which it has not been recorded, it occurs in all the localities from which *L. viridis* and *L. pedunculata* have been collected. *L. viridis* is restricted to S. Portugal (south of Coimbra) and Madeira. Typical *L. pedunculata* occurs in Spain and also in NE. Portugal, but is replaced in S. Portugal, Madeira, and the Azores by a form intermediate between the type and *L. Stoechas*; both type and variety have been collected in Morocco; diverse examples of this western form have been named var. *maderensis* by Bentham (in DC. Prodr. XII, p. 144) and *L. atlantica* by Braun-Blanquet and Maire (Bull. Soc. Hist. Nat. Afr. Nord, XIV, p. 77; 1923). Hybrids of *L. pedunculata* and *L. Stoechas* are recorded from Spain, and of these *L. elongata* Merino (in Brot. Sér. Bot. XII, p. 98; 1914) from Galicia and *L. Cadevallii* Sennen (in Bol. Soc. Arag. XI, p. 231; 1912) from Barcelona correspond closely with the western form of *L. pedunculata*. This latter cannot be explained as a hybrid, however, as true *L. pedunculata* is absent from S. Portugal and Madeira, and the western form occurs alone in the Azores (though other species may, of course, have been overlooked by the few collectors in the Azores). The plants show none of the characters of *L. viridis* which one would expect if they were the hybrid *L. Stoechas* \times *L. viridis*; and *L. viridis* does not occur in the Azores or in Morocco. A variety of *L. pedunculata* occurs in E. Thrace and W. Asia Minor, together with *L. Stoechas*; but this eastern form—*L. pedunculata* var. *cariensis* Benth. (in DC. Prodr. XII, p. 144; 1848) or *L. cariensis* Boiss. (Diagn. Ser. I, v. p. 3; 1844)—is quite distinct from *L. Stoechas*, and indeed resembles typical *L. pedunculata* very closely. Neither hybrids nor intermediates have been recorded.

The explanation of this apparently unstable condition of the species in S. Portugal, Morocco, and the Atlantic Islands is not easy to find. Hybridization does not seem to account for it.

1. *L. DENTATA* Linn. Sp. Pl. p. 572 (1753).

Leaves linear or oblong, pectinate- or pinnate-dentate or crenulate, margins \pm revolute. *Indumentum* of young stems, leaves, and peduncles short, \pm pubescent to densely white-tomentose, the peduncles often lanuginous below the spike. *Peduncles* rather long, usually 5–10 cm., reaching 23 cm.; *spike* lax, cylindrical. Fertile *bracts* 5–12 mm. long, oblate, broadly obovate or ovate, margins entire, \pm apiculate, usually tinged with purple, imbricate. In most

inflorescences there is a gradual transition from normal fertile bracts to the enlarged ovate-elliptic or lanceolate purple or blue-purple sterile bracts of the coma. *Calyx* tubular at flowering period, 5-lobed, the four anterior lobes short and broad, tricuspidate, the median posterior lobe appendiculate, oblate to rotund, clasping the rear of the corolla-tube and the two posterior calyx-lobes; calyx scarcely increasing in length in fruit, enlarging slightly at the base. *Corolla* purple; tube slightly longer than the calyx. *Nucules* 1·25 mm. long, oblong; white areole minute, transversely elliptic.

Distribution. Europe. SPAIN : Cadiz, Gibraltar, Malaga, Grenada, Almanzora, Cartagena, Valencia, Barcelona (*Willkomm* 1258, *Reverchon* Pl. d'Andal. 516, *Huter, Porta & Rigo* 602, 677); Gibraltar (*Lemann, Gamble* 28211). Balearic Islands, Majorca (*Sennen* Pl. d'Esp. 3620 *Porta & Rigo, Bourgeau*). ITALY : (without loc.); Sicily (*Hooker*). GREECE : Corfu, Zacynthos (probably not spontaneous).

Orient. ARABIA : Yemen (*Botta*); Hejaz (*Schimper* 1024).

N. Africa. ALGERIA : Oran, Santa Cruz, Djebel Santo, Cherchel (*Soc. Fr. Duffour*, 194; *Maire*). MOROCCO : Tangier and Tetuan, Mogador, Greater and Anti-Atlas (*Nevaia Hooker*; *Maire*).

Atlantic Islands. MADEIRA : CANARY IS. : Teneriffe (*Bourgeau* 316), Grand Canary, Lanzarote, Gomera (*Bourgeau*). CAPE VERDE IS. : San Antonio (*Bolle*).

NE. Tropical Africa. ABYSSINIA-ERITRAEA borders : Dendera (*Schimper* 624).

Synonyms.—*Stoechas dentata* Mill. *Gard. Dict.* ed. 8, no. 3 (1768); *Reichb. f.* in *Oestr. Bot. Wochensbl.* VII, p. 161 (1857). *L. pinnata* Moench. *Meth. Suppl.* p. 135 (1802). *L. santolinaefolia* Spach in *Jaub. & Spach, Illustr.* iv, p. 111, t. 373 (1850-53).

The last plant appears to be indistinguishable from the more xerophytic types of *L. dentata* L. Dissections of the flowers showed no differences, the leaf- and stem-characters are similar.

Varieties and discussion.—Variation commonly occurs in the shape and indumentum of the leaves, and in the size of the whole plant. The leaf-margin may be much revolute, so that the lower surface of the lamina is almost entirely concealed (this is typical of the young leaves, but may persist throughout their life) or the lamina may be almost plane. The indumentum of much revolute leaves is \pm tomentose, that of the plane leaves is sparsely hirsute. Both characters are probably correlated with the habitat, the rolled tomentose type being xerophytic. The flowers are sometimes white (*forma albiflora*) or pink (*forma rosea*): forms with more numerous sterile bracts than is usual have been collected (*forma multibracteolata* *Sennen ms.*, Morocco).

Var. β . BALEARICA *Ging. Hist. Nat. Lav.* p. 139 (1826).

Plants of dwarf habit, the leaves small, much revolute, sparsely tomentose, spikes and peduncles shorter than those of the type. This is a fairly distinct variety, though intermediates between variety and type occur.

Distribution. Europe. SPAIN : Balearic Is. ; SE. Spain.

N. Africa. ALGERIA.

Var. γ . CANDICANS Battandier in Batt. & Trabut, Fl. Alg. p. 666 (1890).

Leaves, young stems, and peduncles white tomentose to lanuginous : leaf-margins usually much revolute : leaves often rather large.

Distribution. N. Africa. ALGERIA : Coastal regions (Soc. Dauph. 4636 Batt.) ; MOROCCO : Aonina (*Ibrahim*), Mogador, Cap Ghir (*Maire*).

Atlantic Is. MADEIRA : Paul (*Lowe*) ; CAPE VERDE Is. : Cumbre San Antoine (*Bolle*).

2. L. STOECHAS Linn. Sp. Pl. p. 573 (1753).

Upper leaves lanceolate-elliptic, margins slightly revolute, with linear much revolute fastigiate leaves in their axils and at base of branches. *Indumentum* of whole plant short, white, \pm dense tomentose, glands not apparent. *Peduncles* short, usually 1-2 cm., up to 3.5 cm. *Fertile bracts* broadly ovate, oblate to spathulate-obovate, apiculate or shortly acuminate, base of upper bracts attenuated into a short petiole. Sterile bracts of *coma* purple or occasionally white, obovate or spathulate, broadly obtuse at apex, exceeding fertile bracts by 1-2 cm. occasionally by 3 cm. *Calyx* ovate at flowering stage, increasing in length in fruit. *Corolla* black-purple or occasionally white, pink, or coppery pink : tube 1-2 mm. longer than the calyx. *Nucules* broadly elliptic-oblong, 2 mm. long, with thin gelatinous coat when boiled.

Distribution. Europe. FRANCE : E. Pyrenees (*Schultz* 536 bis), Narbonne (*Endress*), Marseilles, Perpignan, Montpellier (*Planchon*), Toulon, Var (Le Luc *Schultz* 536), Hyères, Cannes, Nice, Mentone. Corsica ; Bonifacio, Bastia (*Gandoger*), Trinitá. PORTUGAL : Lisbon, Coimbra (Herb. Hort. Bot. Coimbr. 258), Trans-Tagus, Arravidá monastery, Algarve (*Faro Bourgeau* 1994). SPAIN : Barcelona (*Sennen*), Valencia, Malaga, Algeciras, Gibraltar, Cadiz, Cordova, Galicia. Balearic Is. Minorca. ITALY : Bordighera, Etruria, Port Ercole, Florence, Pisa. Sardinia ; Tempio, Golfo degli Aranci. Ins. Caprera. Isle of Elba. Sicily ; Palermo, Segetum, Alcamo. CRETE, Meleka, Lakkoi (*Atchley* 1415). GREECE AND AEGEAN IS. : Hymettus (*Orphanides* 273), Theodoroi Athea, Phodele, Calauriac, Zaczynthos, Idrae, Lyra, Skopelos, Melos, Kimolos, Corfu. Greek MACEDONIA : Sithonia Penins. THRACE : Radi Reni, Gallipoli ; Constantinople (*Noé* 398). DALMATIA ; Ragusa.

Orient. ASIA MINOR : Princes Is. (*Gilliat-Smith* 1263) ; Bithynia ; Lydia, Smyrna (*Bornmüller* 9852 b) ; Cilicia (*Péronin* 72 and *Siehe* 54) ; Troy, Mt. Ida (*Sintensis* 666). CYPRUS : Kophino, Péra, Korno, and Lef Kara. SYRIA : Beyrout (*Hooker*), Saïda, Plain of Antioch, Mt. Cassius. PALESTINE : Ain Zehalta, Hermon, between Jaffa and Asdod (*Bornmüller* 1242), Leontes valley, Ramleh, Lebanon.

N. Africa. ALGERIA : Alger and Oran provinces. MOROCCO : Greater Atlas (*Hooker*), Mogador (*Hooker*), Agadir (*Hooker*), Rabat, Tangier, and Tetuan, Marmora forest near Rabat.

Atlantic Is. MADEIRA : CANARIES : Teneriffe, Orotava (*Lowe* 111), Laguna, Cumbre de Anaga.

Synonyms.—*Stoechas officinarum* Mill. Gard. Dict. ed. 8, no. 1 (1767); Reichb. f. in Oestr. Bot. Wochensbl. VII, p. 161 (1857). *Stoechas arabica* Garsault, Fig. Pl. Anim. Med. t. 45 (1764) et Descr. Pl. Anim. p. 35 (1767); Thell. in Bull. Herb. Boiss. Sér. 2, VIII, p. 783 (1908). *L. incana* Salisb. Prodr. p. 78 (1796). *L. stoechadensis* St. Lag. in Ann. Soc. Bot. Lyon, VII, p. 128 (1880).

The last name was suggested for grammatical reasons and refers to no actual specimens.

Variations and discussion.—The original binomial *L. Stoechas* Linn. included, as var. β , the modern *L. pedunculata* Cav., which was separated off as a distinct species by Cavanilles in 1802. The species proper has since then been divided by various authors into a number of varieties. Gingins de Lassaraz (op. cit. p. 130; 1826) made 3 varieties, which he named *brachystachya*, *macrostachya*, and *leucantha*; the first two seem to me hardly sufficiently distinct to necessitate the division, the last is the albino form, a pathological condition rather than a structural variety. Plants have been collected bearing both white and normal spikes (e.g. E. Pyrenees, near Villefranche, *Ellman & Sandwith* 93). Albino forms are fairly frequent; the corolla is occasionally coppery pink, forma *rosea* Maire (Bull. Soc. Hist. Nat. Afr. Nord, p. 223; 1933), from Algeria. Since Gingins de Lassaraz several varieties have been named, and though the plant undoubtedly does vary considerably in indumentum, leaf-size and shape, and size and shape of spike and coma, the various types seem inconstant and not clearly defined, and I have not maintained the varieties here. There are two curious specimens in the Kew Herbarium, collected by Lowe (26. iii. 1862 and 14. vi. 1872, both no. 363) from Madeira. These specimens show resemblances to *L. Stoechas* and *L. viridis* and are probably hybrids. The leaves, their indumentum and that of the young stems and peduncles are intermediate between *L. Stoechas* and *L. viridis*; the peduncles are short, similar to those of *L. Stoechas*; the fertile bracts rotund dentate to broadly ovate or spathulate-obovate entire, \pm deep purple; sterile bracts obovate to obovate-oblong, pallid in one specimen, darker purple in the other; posterior calyx-appendage larger and more conspicuous than is usual in *L. Stoechas*; corollas of the earlier specimen noted as black-purple or black, the other probably white, resembling *L. Stoechas* and *L. viridis* respectively. The inflorescence is remarkably lax, having a superficial resemblance to that of *L. dentata*, but the spike of *L. Stoechas* varies considerably in density. Lowe named both the plants *L. viridis* Ait. (*L. viridis* L'Hérit.), and qualifies the earlier specimen as ' α fl. atropurpureis fere atris, bracteis late violaceis'. These plants are neither typical *L. Stoechas* nor *L. viridis*, and are probably hybrids of the two.

3. *L. VIRIDIS* L'Hérit., Sert. Angl. p. 19, t. 21 (1788).

Leaves sessile, often uniformly linear-elliptic to linear-lanceolate, sometimes linear and fastigate at the base of the branches, margins \pm revolute. *Indumentum* of whole plant \pm densely hirsute of short asperous greenish hairs, not grey

tomentose (except occasionally on young stems). *Peduncles* of medium length, up to 7·5 cm. *Spike* usually robust. *Fertile bracts* obovate, rotund, or broadly ovate, margins almost entire, slightly crenulate, dentate, apiculate or emarginate, tomentose-ciliate; greenish-white or white. *Sterile bracts* of *coma* oblanceolate or narrowly elliptic, white or greenish white. *Calyx* broadly tubular in flowering stage, becoming \pm ovate and increasing in length in fruit. *Corolla* white, the tube slightly longer than the calyx. *Nucules* rotund-oblong, compressed.

Distribution. Europe. PORTUGAL: Algarve, Sierra Monchique (*Welwitsch* 276, *Bourgeau* 1933), Villa Nova (*Trevelyan*), Alemlejo (*Daveau* 1187).

Atlantic Islands. MADEIRA (*Masson*), Currhal Velha (*Mason*), Capo Garajão (*Kuntze*, *Clarke* *139).

Synonyms.—*L. viridis* Aiton, Hort. Kew. II, 288 (1789). The description of L'Héritier is quoted exactly by Aiton. *L. Massoni* Cels ex. Ging. Hist. Nat. Lav. p. 137 (1826). *L. pseudostoechas* Reichb. ex Holl in Flora, 1829, p. 691. See under *L. pedunculata* var. *maderensis* Benth.

Discussion.—*L. viridis* stands mid-way between *L. pedunculata* and *L. Stoechas*, but it is distinguished from both by its more hispid, green indumentum, rather longer, more uniform leaves, white or greenish-white spikes, and by its rotund-oblong nucules. The plants must be quite easily distinguishable in the living state, but dried specimens lose their colour and are easily confused with the short peduncled form of *L. pedunculata* var. *maderensis* Benth.

4. *L. PEDUNCULATA* Cav., Descr. p. 70 (1802).

Upper leaves elliptic-lanceolate, slightly revolute, with linear much revolute \pm fastigiate leaves in their axils and at base of stem. *Indumentum* of leaves \pm densely short grey tomentose, usually glandular; of peduncles and young stems shortly hirsute to densely white tomentose. *Peduncles* typically long, 10–20 cm. up to 32 cm. *Fertile bracts* large, the lowest pair 6–12 mm. long; oblate, very broadly obovate to almost triangular, the distal margin usually broadly dentate, tricuspidate, or almost entire, occasionally apiculate; indumentum short, sparse, hispid, margins shortly tomentose-ciliate; lowest bracts sessile, the upper shortly petiolate. *Coma* purple or sometimes white, of sterile lanceolate elliptic or narrowly oblanceolate bracts, up to 3·5 cm. longer than the fertile bracts. *Calyx* tubular, 5–6 mm. long, increasing in fruit to \pm 8 mm., becoming urceolate. *Corolla* deep purple or sometimes white, tube only slightly longer than the calyx. *Nucules* oblong, 2 mm. long, lacking a gelatinous envelope when soaked in water.

Distribution. Europe. SPAIN: Galicia, Escorial (*Lange*), Aragonese Pyrenees (*Billot* 2117, rather dwarf specimen), Madrid (*Reuter*, *Bourgeau* 2184), Castille, Valencia (*Sierra Sacaño Reverchon* 680), Jaen (Herb. Gay 318), Cordoba (*Lange*), Toledo, Palencia (*Alar del Rey*, *Levier*).

Varieties of *L. pedunculata* occur in Spain, Portugal, Thrace and Asia Minor, Morocco, Madeira, and Azores,

Synonyms.—*L. Stoechas* var. β , Linn. Sp. Pl. p. 573 (1753). *Stoechas pedunculata* Mill. Gard. Dict. ed. 8, no. 2 (1768); Reichb. f. in Oestr. Bot. Wochensbl. VII, p. 161 (1857).

Varieties.

β . *CARIENSIS* Benth., in DC. Prodr. XII, p. 144 (1848).

Leaves small, linear, much revolute, and narrowly elliptic-lanceolate, scarcely revolute. Indumentum of leaves shortly villous or tomentose, more sparse than is usual in *L. pedunculata*; of peduncles and young stems hirsute or tomentose, hairs longer and very densely white-lanuginous below the spike. This indumentum differs from that of *L. pedunculata* in the greater length of the hairs and in its more hispid nature. Boissier (Diagn. Ser. i, v, p. 3; 1844) describes the indumentum as green, but this is not apparent in dried material. The indumentum of the spike, especially the margins of the fertile bracts, is more densely tomentose than that of *L. pedunculata*. Peduncles are usually long, up to 23 cm. Bracts oblate to broadly obovate, the distal margin dentate, undulate, or almost entire, sometimes minutely apiculate, resembling *L. pedunculata*, sensu stricto. Coma pallid or violet. Calyx tubular, the posterior appendage entire or denticulate. Corolla violet, rather larger than that of *L. pedunculata*; corolla-tube up to 1·5 mm. longer than calyx. Nucules broadly oblong, 1·75 mm. long, shorter and broader than those of the type, with a thin gelatinous coat when boiled.

Distribution. BALKAN PENINSULA: Thrace (Constantinople Clementi, Istanbul Balls B 2377, Turkey in Europe Thirke, Therapia Thuret).

ASIA MINOR: Birghui (Tmolus occid. *Balansa* 326), Bithynia (Bornmüller 5437), Caria (Pinard), (Aucher 1763).

Synonym.—*L. cariensis* Boiss. Diagn. ser. I. v. p. 3 (1844).

Boissier says his plant differs from *L. pedunculata* in the sparser indumentum, lobed (not entire) calyx-appendage, pallid (not intensely violet) coma, and corolla-tube not exceeding calyx; but, as Bentham (loc. cit. above) remarks, in a specimen collected by Aucher (no. 1763) the indumentum is canescent, the spike as *L. pedunculata*, and the calyx-appendage transversely oblong stipitate, entire. The great gap in distribution, however and the various minor structural differences seem to warrant the status of variety, though not that of species.

L. spectabilis Koch in Linnaea, XXI, p. 646 (1848).

Koch himself originally named the plant collected by Thirke (type of *L. spectabilis* Koch) *L. cariensis* Boiss. (in Linnaea, XIX, p. 24; 1847), but later altered this to *L. spectabilis* Koch (loc. cit.) and provided a description. His plant was said to differ from *L. cariensis* Boiss. in its violet coma, and corolla greatly exceeding the calyx. The first of these characters occurs also in

L. pedunculata, the second resembles neither *L. pedunculata* nor *L. cariensis*, but in a specimen collected by Thirke from Turkey-in-Europe in Herb. Boissier the corolla-tube only exceeds the calyx by about 1-1.5 mm. Boissier (in Fl. Or. iv, p. 541; 1879) reduces *L. spectabilis* to *L. cariensis*, quoting Thirke's specimens, and indeed the two plants are almost identical.

There are variations of size of bract and of indumentum of bract and peduncle which are common to those varieties of *L. pedunculata* which occur in N. Spain, S. Portugal, Morocco, Madeira, and Azores. These differ as a whole from the type in their smaller fertile bracts, the margins long grey tomentose, and in their tomentose peduncles, lanuginous below the inflorescence. These deviations from the normal *L. pedunculata* type approach *L. Stoechas*; such intermediates may indicate a common ancestry for the two species, but are not explicable as hybrids (see under discussion of Section *Stoechas*, p. 161 above).

γ. MADERENSIS Benth. in DC. Prodr. XII, p. 144 (1848).

This variety differs from *L. pedunculata* proper in the *indumentum*, tomentose on the leaves, villous on the peduncles and young stems, becoming lanuginous below the inflorescence, more densely tomentose on the inflorescence, especially the margins of the fertile bracts, in the shorter *peduncles* (3.5-13 cm.), and in the spathulate or oblanceolate, rather shorter, sometimes paler violet, sterile bracts of the *coma*. The fertile bracts though smaller resemble those of *L. pedunculata*.

The specimens on which Bentham based his var. *maderensis* were collected by Lemann in Madeira. He described them as intermediate between *L. pedunculata* and *L. viridis*, and indeed one of the specimens collected by Lemann (now in Herb. Benth. at Kew) resembles *L. viridis* very closely. None of the other specimens from Madeira at Kew or in Herb. Boissier or Barbey-Boissier at Geneva are true *L. pedunculata*, which here appears to be represented only by the var. *maderensis*.

Distribution. ATLANTIC IS. AZORES (Flamingos, Fayal Watson 142). MADEIRA (Lemann, Mason, Clarke 139, Palheiro Hooker).

Synonym.—*L. pseudostoechas* Reichb. ex Holl in Flora, 1829, p. 691.

The type-specimen of *L. pseudostoechas* was collected by Holl in Madeira. It was described by Reichenbach (l.c.) as differing from *L. Stoechas* "durch eine gewöhnlich lang gestielte Aehre, und durch abgestumpfte Bracteen". Bentham (in DC. Prodr. XII, p. 144; 1848) places *L. pseudostoechas* under *L. Stoechas* var. β . *macrostachya*, but as Briquet points out (Lab. Alpes Marit. p. 463; 1891), from the original diagnosis the plant does not properly belong to *L. Stoechas* at all. The plant can only have been *L. pedunculata* var. *maderensis* Benth. or *L. viridis* L'Hérit. Menezes (As Lab. Mad. p. 4; 1907) mentions *L. pseudostoechas* as a synonym of *L. viridis*.

$\delta.$ ATLANTICA (*Br.-Bl.*) *Jahand.* & *Maire*, Cat. Pl. Maroc. p. 622 (1934).

In the original description plants of this variety are described as compact dwarf bushes, 20–30 cm. high, but the variety has been slightly extended to include larger forms. The leaves resemble *L. pedunculata*, the larger are oblong-lanceolate, up to 4 cm. long, 3–5 mm. broad, with smaller fastigiate linear leaves in the axils and at the base of the stems. The indumentum of the leaves and young stems is very short tomentose-pubescent of flexed branching hairs, that of the peduncles is \pm densely tomentose becoming lanuginous near the inflorescence; glands are not evident. The peduncles are 3–10 cm. long. The fertile bracts are reniform rounded or rotund-ovate entire or dentate, smaller than those of *L. pedunculata*, the basal pair sessile, those above shortly (\pm 2 mm.) petiolate; the indumentum hirsute, long dense tomentose at the margins, unlike that of *L. pedunculata*. Sterile bracts of coma up to 3 cm. long, lanceolate, acuminate, pale violet. Calyx tubular at flowering stage, 4–5 mm. long, teeth very short, the posterior appendage \pm cordate. Corolla violet, puberulent.

Distribution. Europe. SPAIN : Leon (Winkler, Villa Franca de Viergo).

N. Africa. MOROCCO : Atlas (Roria Maw, Asfaton Maire), High Atlas (Ait Mesan Ball, Demnat Braun-Blanquet, Azrou Jahandiez).

Synonyms.—*L. Stoechas* subspecies *atlantica* Br.-Bl. in Bull. Soc. Hist. Nat. Afr. Nord, xiii. p. 191 (1922). *L. atlantica* Br.-Bl. in Bull. cit. xiv, p. 77 (1923).

Dr. Braun-Blanquet in his 'Contributions à l'étude de la Flore marocaine' just quoted gives an excellent description of this plant, and compares it with *L. Stoechas* and *L. pedunculata*. He concluded originally that it was a subspecies of *L. Stoechas*, but after studying further material he raised it to species-rank in a note published in 1923 (loc. cit.). The plant is one of the western forms of *L. pedunculata*, and is comparable to the var. *maderensis* Benth. from Madeira and the Azores.

$\epsilon.$ LUSITANICA *Chaytor*, var. nov.

Foliis et pedunculis et bracteis a planta typica differt. Folia oblongo-linearia, usque ad 4·5 cm. longa, marginibus vix revolutis, indumento breviter tomentoso-pubescente sparsiore, ramis in parte infimo foliis paucis minoribus linearibus fastigiatis praeditis. Pedunculi 3·5–12 cm. longi, plus-minusve tomentosi, superne lanuginosi. Bractae fertiles plus-minusve orbiculares apiculatae, eis *L. pedunculatae* minores marginibus tomentoso-ciliatis; bractae superiores (coma) lineari-ellipticae, acutae; coma usque ad 2·2 cm. longa in vivo probabiliter pallide violascens.

Distribution. Europe. PORTUGAL : Algarve (Faro Bourgeau 1994), Trafaria (Daveau 3086), Coimbra (Ferreira, Herb. Hort. Bot. Coimbr.).

Approaching the type is a specimen from Portugal, Coimbra (Herb. Hort. Bot. Coimbr. 242) : it resembles the variety in its leaves, indumentum, and fertile bracts, but the peduncle-length and sterile bracts approach the type. It is intermediate between var. *lusitanica* and the type in station as well as in morphological characters.

HYBRIDS OF SECTION STOECHAS.

L. STOECHAS Linn. \times L. PEDUNCULATA Cav.

\times L. CADEVALLII Sennen in Bol. Soc. Arag. xi, p. 231 (1912), et in Bull. Géogr. Bot. p. xxiv, 227 (1914).

Habit intermediate between the parents ; large leaves fewer than is typical of *L. pedunculata*, small narrow leaves numerous, resembling *L. Stoechas* in arrangement and indumentum. Peduncles intermediate, 2–9 cm. Spikes robust, compact, oblong, up to 5·5 cm. including coma up to 2 cm. Fertile bracts intermediate, 5–6 mm., \pm rotund, margin slightly dentate or entire broadly obtuse, hirsute, margins sparsely tomentose-ciliate ; sterile bracts of coma obovate or broadly oblanceolate resembling *L. Stoechas*, \pm tomentose hirsute.

Distribution. Europe. SPAIN : Catalonia, near Barcelona. (Tibidabo, Sennen 2791, Bonanova Sennen 1766, Can Ferrer Sennen Soc. Fr. Exs. Duffour 3120.)

\times L. ELONGATA Merino in Brot. Sér. Bot. xii, p. 98 (1914).

This hybrid of *L. Stoechas* with *L. pedunculata* was originally described as a variety of *L. Stoechas*, as var. *elongata* Merino, Fl. Galic. II, p. 190 (1906), as follows : ‘Pedunculi 8–12 cm. longi ; spica angustior ; comae bracteae longiores ; planta inter hanc et sequentem speciem [i.e. *L. Stoechas* and *L. pedunculata*] quasi media.’ Later, in ‘Broteria’ (i.e. above) Merino altered the variety to a hybrid species *L. elongata*. In a note he says that the plant shows all the characters of a hybrid product of *L. Stoechas* and *L. pedunculata*, amongst which it was found ; the peduncle, 3–12 cm. long, is distinctly shorter than that of *L. pedunculata*, the sterile bracts agree in shape with those of *L. Stoechas*, but are generally narrower and longer.

Collected in N. Spain, Galicia, San Cipriano, Lugo to the mouth of R. Miño by Merino, exsicc. 954.

\times L. PANNOSA Gand. in Bull. Soc. Bot. Fr. XLVIII, p. 411 (1901).

The original description is as follows :—‘ Tota incano-tomentella vel effuse floccosa. Mixta inter *L. stoechadem* et *L. pedunculatam* ; ab utraque differt foliis crassis parum nervosis, caulis stricto-virgatis, spica laxiore haud aut vix comosa, bracteis valde elevatim nervoso-reticulatis undulatis obtusissimis vel retusis, calyce late costato, corolla atrata parva, odore non camphorato.

‘ SPAIN, Caceres, in Sierra de San Pedro.’

There is a specimen in the Kew Herbarium (coll. Welwitsch 97) from Estramadura in Portugal, which differs from *L. pedunculata* and *L. Stoechas* in its long leafy shoots, the leaves long (up to 4·5 cm.) narrow oblong-linear, margins scarcely revolute, with comparatively few small linear much revolute basal and axillary leaves. Peduncles and fertile bracts intermediate between the two species. The plant is probably of hybrid origin.

L. PEDUNCULATA Cav. × L. LATIFOLIA Vill.

× *L. ELIAE* Sennen in Bol. Soc. Iber. XXXI, p. 16 (1932). I have not seen material of this hybrid. The original description is as follows:—‘*Folia canescentia ; rami floriferi breves, non semper quadrangulares interdum cylindrici sulcatique ; bracteae latae, venosae, reticulatae, denticulatae.*’

‘Feuilles canescentes en denses fascicules sur le vieux bois, abondantes à la base des rameaux florifères courts-robustes non toujours quadrangulaires, mais parfois cylindriques-sillonnés-vergetés ; feuilles extérieures étroitement connées—les bases unies par un mince cordon, cunéiformes lancéolées reticulées revolutées, longues, 3 cent. et plus, par 3–4–5 paires à la base des rameaux plus ou moins coudés ; épis subconiques, épais et longs. $4\frac{1}{2} \times 2$ cent. environ ; bractées larges veinées reticulées denticulées, d'un violet clair, laissant poindre les corolles, non ou peu les points des sépales non argentées-laineuses, comme on les aperçoit sur les épis d'un violet obscur du *L. pedunculata* ; bractées du sommet en panache peu apparent.

‘SPAIN, Burgos, Val de Besantes, “inter parentes,” leg. Hno. Elias.’

L. DENTATA Linn. × L. OFFICINALIS Chaix, and L. DENTATA Linn. × L. LATIFOLIA Vill.

× *L. HETEROPHYLLA* Poir. Encycl. Meth. Suppl. III, p. 308 (1813).

Leaves sessile or shortly petiolate, linear or elliptic, on each plant the margins of some leaves entire, of others partially dentate, with 1–7 teeth on each side at about the centre or towards the apex, margins slightly revolute. *Indumentum* of stems and leaves short grey tomentose or pubescent. *Spike* cylindrical, often interrupted at the base. *Bracts* ovate, acute. *Corolla* small, bluish. *Coma* absent.

L. heterophylla was originally described as a hybrid of *L. dentata* with *L. spica* Linn. This latter is presumably the species as mentioned by Lamarek earlier in his *Encyclopédie* (III, p. 427; 1791) including the two species *L. officinalis* Chaix and *L. latifolia* Vill.

Gingins de Lassaraz (op. cit. p. 142; 1826) divides *L. heterophylla* into two varieties:—

α. Leaves narrow, elliptic or linear, pubescent, greenish grey ; plant robust ; spike interrupted, narrow, cylindrical, bracts uniform. Cult. in Hort. Reg. Paris, 1815.

β. Leaves broad, lanceolate to spatulate, tomentose, lower internodes short, leaves crowded ; plant small ; spike compact, uppermost bracts slightly enlarged, ± comose, purple. Cult. in Hort. Bot. Dinegro Genovae (*Viviani*, *Lindley* (1828) ex *Viviani*).

Synonym.—*L. hybrida* Balbis in herb. DC. (1825), cult. Turin (1816). I have not traced a description. Gingins de Lassaraz quotes *L. hybrida* as a synonym of var. β.

Gingins de Lassaraz suggested that his var. α had the parentage *L. dentata* Linn.

$\times L. officinalis$ Chaix and his var. β . $L. dentata$ Linn. $\times L. latifolia$ Vill. Poiret's original description of $L. heterophylla$ agrees best with plants of the former parentage, i.e. with Gingins de Lassaraz's variety α . Plants of the latter parentage can, if desired, be given the binomial $L. hybrida$ Balbis ex Ging.

These hybrids do not seem to occur in the wild state, but are reported only from botanic gardens.

$\times L. ALLARDI$ Hy in Bull. Herb. Boiss. III. Append. 1, p. 16 (1894).

A hybrid of $L. dentata$ Linn. with $L. latifolia$ Vill. The leaves are linear to oblong-spathulate, dimorphic, some entire, others partially dentate towards the apex : plant robust tall, internodes long, nucules abortive. $L. Allardi$ also differs from $L. latifolia$ in its broadly lanceolate, thin, plane, greenish-grey pubescent bracts, and from $L. dentata$ in the uniformity of the bracts, the uppermost not enlarged comose, in the presence of bracteoles, and in the interrupted rather more slender spike.

Distribution. Europe. FRANCE : Maine-et-Loire ' spontaneously in garden of Maulevrie ', (Hy nos. 422 & 4015).

The parentage of $L. Allardi$ as given by Hy agrees with that of $L. heterophylla$ Poir. var. β . Ging., but his specimens differ from the latter in size, habit, and length of lower internodes, and in spike and bract characters, and seem to agree more closely with the original description of $L. heterophylla$ and with the var. α Ging.

SECTION II. SPICA Ging. Hist. Nat. Lav. p. 141 (1826).

Original diagnosis.—' Charact. Calyx appendiculatus, flores verticillatospicati, bracteis remotis multifloris, floribus bracteolatis, spica non comosa.

Observ. Caulis superne nudus. Calyx dente superiore appendiculato ; tubus corollae calyce saepissime duplo longior ; limbus bilabiatus, labio superiore sub-latiore bifido ; labio inferiore 3-lobo ; stamna inclusa. Caryopsides adnatae minutae oblongae, laeves, area umbilicali minuta. Arbusculae.'

The habit of species of the section Spica is bushy, reaching about 1 metre in height, the base woody, the old bark peeling off in flakes and strips.

The leaves are linear-lanceolate or spathulate, entire. Indumentum of young shoots and leaves dense grey tomentose, often becoming more sparse with age. The peduncle is usually long (\pm 10–60 cm.) simple or branched. The spike is unbranched compact or interrupted, cylindrical. The bracts are \pm uniform in each spike, all fertile, with a contracted cyme of 3–7 flowers in each axil ; arranged in exactly opposite pairs. The presence of bracteoles is diagnostic for the section. The calyx is almost sessile or shortly (up to 3 mm.) pedicellate ; 8- or 13-nerved, 8- or 5-toothed, the posterior tooth enlarged into a rotund lanceolate ovate or elliptic appendage. The corolla is bilabiate, 2 lobes above and 3 below, the posterior lobes much the larger, upright ; corolla-tube about double calyx-length. The nucule is elliptic or oblong, areole small, white ; no gelatinous envelope when wet.

KEY TO SPECIES OF SECTION SPICA.

Young stems and leaves short grey tomentose, older parts usually becoming glabrescent; calyx 13-nerved, 5-dentate.

Peduncles typically unbranched; bracts broad, ovate to \pm rotund, apiculate, scarious 5. *L. officinalis*.

Peduncles typically branched; bracts narrow, linear to linear-lanceolate, herbaceous 6. *L. latifolia*.

Whole plant grey tomentose, leaves of all ages lanuginous-tomentose; calyx 8-nerved, 8-dentate 7. *L. lanata*.

DISCUSSION OF SECTION SPICA.

L. officinalis and *L. latifolia* have been cultivated in temperate regions for many centuries, and in the course of time hybridization and artificial selection have resulted in the stabilization of several garden forms. It is hoped to deal more fully with these cultivated lavenders later on, but some of the hybrids found in nature (and also in gardens) are considered here.

The distribution of species of section *Spica* in the wild state is confined to the NW. Mediterranean regions, i.e. SE. and E. Spain; Balearic Isles; in France, E. Pyrenees, southern maritime provinces and Dordogne, Lot, Dauphiné, Rhône, and Doubs; W. Switzerland; N. and N.-central Italy; Corsica; Sicily; Istria and Dalmatia. (Desfontaines recorded localities in the Atlas Mts. of Morocco, but these have never, so far as I know, been confirmed.)

5. *L. OFFICINALIS* *Chaix* in Vill. Hist. Pl. Dauph. I, p. 355 (1786), and II, p. 363 (1787).

Leaves usually dimorphic, those at the base of the stems and in the leaf-axils on the young shoots small, much revolute, \pm fastigiate, dense grey tomentose, primary leaves of young shoots larger, up to 6 cm. long and 0·6 cm. broad, glabrescent, margins scarcely revolute; the leaves are narrower than those of typical *L. latifolia*; glands are present principally on the lower surface. Peduncles unbranched (sometimes with short slender branches, though such plants are probably of hybrid origin), erect, shorter than those of *L. latifolia*. Spike \pm compact or interrupted especially at the base, the lowest verticil usually distant from the rest. Bracts membranous, ovate, very broadly ovate to obovate, acuminate or apiculate, almost glabrous, shortly and sparsely pubescent or hispid, especially on the nerves, usually about half as long as the calyx; median and two or three pairs of lateral nerves conspicuous. Bracteoles very small, linear, brown, scarious. Calyx about 5 mm. long, 13-nerved, marginal teeth very short and rounded, or margin nearly entire, posterior appendage oblate or rotund, often deep purple; indumentum \pm dense tomentose-lanuginous tinged with purple, especially in young flowers. Corolla-tube nearly double the calyx length, \pm 9 mm., lobes large. Nucule narrowly oblong, 2·73-3 mm. long.

General distribution. Europe. NE. SPAIN; Pyrenees; SE. FRANCE; SWITZERLAND; N. ITALY; CORSICA; DALMATIA, Istria (? cult.).

(N. Africa: Atlas Mts. Desf. Fl. Atl. II, p. 12 (1800), though it is not mentioned in later works and I know of no specimens.)

The species and various varieties and hybrids are cultivated in most temperate countries of the world.

Varieties.

α. ANGUSTIFOLIA *Rouy & Fouc.* Fl. Fr. XI, p. 255 (1909).

This variety is distinguished by its small size and slender stems 20 to 30 cm. high, linear leaves with revolute margins, and rather short slender spikes.

Distribution. Europe. FRANCE (Lyon *Jordan*, Dauphiné near Briançon *Sieber* 133, cult. Grenoble from Gap, Soc. Dauph. no. 1784, *Verlot*, Couza Lyon *Billot* Fl. Gall. & Germ. exsicc. 709, Besançon Doubs *Billot* exsicc. 1045, Cahors Lot *Billot* exsicc. 1045 bis in Herb. Boissier). ITALY: Piedmont (Tenda, *Reichenbach fil.*), near Modena (Mt. Ventoso, Herb. Gay). DALMATIA: Ragusa (*Kreiger*).

Synonyms.—*L. vera* DC. α *coerulea* (forma) *angustifolia* Ging. Hist. Nat. Lav. p. 147 (1826). *L. spica* Linn. var. \times *angustifolia* Briquet, Lab. Alpes Marit. p. 466 (1895). *L. fragrans* Jord. ap. *Billot*, Annot. p. 171 (1859), exsicc. no. 709.

β. DELPHINENSIS *Rouy & Fouc.* Fl. Fr. XI, p. 255 (1909).

This variety is distinguished from var. *angustifolia* by its larger size, more robust stems, 30–50 cm. high, lanceolate to oblong leaves with scarcely revolute margins, and by its longer, more interrupted, more robust spikes.

Distribution. Europe. SWITZERLAND: near Friburg (Motiers, *de Rutté*), Vaud, Bex. FRANCE: Hautes Alpes (Grave *Billot* exsicc. 2726, Gap *Reverchon*, Roche des Arnands *Neyria*), Isère (Rochefort, Soc. Dauph. No. 2210, *Verlot*), Rhône (Couzon, *Gandoger* 820), Mentone, Nice-La-Chiondola. ITALY: Lombardy (*Porta*), Piedmont (ex herb. Boissier).

Synonyms.—*L. vera* DC. var. α *cærulea* \times *latifolia* Ging. Hist. Nat. Lav. p. 147 (1826). *L. spica* Linn. β *delphinensis* Briquet, Lab. Alpes Marit. p. 466 (1895). *L. delphinensis* Jord. ap. *Billot*, Annot. p. 171 (1859) exsicc. no. 2626.

The two varieties, *angustifolia* and *delphinensis*, are quite distinct when typical examples are compared, but numerous intermediate specimens exist. These may have broad leaves and small stature, narrow leaves and greater height, or medium leaves and medium height. Where such a great range of types exists, it is obviously convenient to name the extremes, but impossible to define exactly the boundaries between them. There are intermediate specimens at Kew from the Hautes Alpes in France, Gap (*Billot* Fl. Gall. & Germ. exsicc. 1045 and 1045 ter), La Grave (*Mathonnel* 763), Briançon (Herb. Gay 133), Isère, Corps, and from Piedmont in Italy.

γ. PYRENAICA Benth. Lab. Gen. et Sp. p. 149 (1832).

This variety is distinguished from the rest of the species by the very large bracts, broadly ovate to oblate acute or apiculate, up to 7 mm. long and 9 mm. broad, often purplish especially at the apex of young spikes. (These bracts vary considerably in size, but are always larger than in the other varieties.) The calyx-indumentum of this variety is short, grey-tomentose, mostly confined to the prominent nerves, not purplish lanuginous-tomentose. The leaves are typically very narrow, linear, but may be oblong-linear or linear-lanceolate. The plants are typically small, young shoots including peduncle and spikes, 15–20 cm. ; but specimens occur with shoots up to 35 cm. high. The taller forms, with broader leaves and often rather smaller bracts than the dwarf plants, have been separated as a distinct variety, var. *Faucheana* (*L. spica* var. *Foucheana* Briquet, Lab. Alpes Marit. p. 467 ; 1895 ; *L. officinalis* Chaix, race *pyrenaica*, var. *Faucheana* Rouy & Fouc. loc. cit.). Intermediate types are so numerous and the two extremes so ill-defined that I have not tried to separate the var. *Faucheana* from var. *pyrenaica*, *sensu stricto*, though the two would form a parallel with the vars. *angustifolia* and *delphinensis*.

Distribution. Europe. SPAIN : Spanish Pyrenees ; Venasque (*Joad, Gay*), Pineda (*Bordère*), Seo de Urgel (*Bentham*), Arandora, St. Julian (*Bourgeau* 651), Cerdagna, Gorgis de Illo (*Sennen*) ; Aragon, Jacca (Herb. Forrestier). FRANCE. Hautes Pyrénées, Gèdre and Lourdes (*Bordère*), Pyrénées Or., Villefranche (*Endress, Sennen*, No. 3682²), Ariège, Sabarat (*Mailho* 2549, this is typical of var. *Foucheana*).

Synonyms.—*L. pyrenaica* DC. Fl. Fr. v, p. 398 (1815). *L. spica* γ. *pyrenaica* Briquet, Lab. Alpes Marit. p. 467 (1895). *L. spica* var. *turoensis* Pau h.b. in Bol. Soc. Iber. xxvii, p. 170 (1928) is said to differ from var. *pyrenaica* in the much larger bracts of var. *turoensis*. Albino plants occur throughout the species.

This species, *L. officinalis* Chaix, is the type of true Lavender of the perfume industry and of gardens, but hybridization with *L. latifolia* and artificial selection for many centuries have affected the cultispecies, and the typical wild forms of *L. officinalis* are seldom seen in cultivation.

6. *L. LATIFOLIA* Vill. Hist. Pl. Dauph. II, p. 363 (1787).

Leaves dimorphic, the primary leaves of young shoots up to 6 cm. long and 1·2 cm. broad, becoming glabrescent, margins scarcely revolute, the basal and axillary leaves rather smaller, ± fastigiate, remaining densely grey tomentose throughout their life, margins scarcely or much revolute. Leaves linear-lanceolate, narrowly elliptic to spatulate, much attenuated at the base, glandular especially on the lower surface. *Peduncles* typically branching, spreading, often very long. *Spike* often interrupted, ± compact, rather slender. *Bracts* herbaceous, linear to lanceolate, acute, tomentose or hispid, equal to calyx or slightly longer ; median nerve alone conspicuous. *Bracteoles* linear, up to 3 mm. long, ± herbaceous, green or greyish. *Calyx* ± 5 mm. long, 13-nerved, marginal teeth obtuse or rounded, posterior appendage elliptic or

ovate, folded or cucullate ; indumentum very short grey tomentose, occasionally tinged with purple. *Corolla tube* \pm 7.5 mm. long, lobes small. *Nucule* broadly oblong, 2 mm. long.

Distribution. Europe. SPAIN : Barcelona (*Sennen* 3765), Teruel (*Reverchon* 645), Valencia (*Reverchon* 645), Murcia (*Gandoger* 346), Jaen, Alcarria, Grenada (*Reuter*), Riopar (*Bourgeau* 812). Balearic Isles ; Majorca. FRANCE : Dordogne, Ariège (*Bordère*), Pyrénées Or., Villefranche (*Endress*), Sardinya (Soc. Dauph. 1326 bis), Aude (*Billot* 2335), Marseilles, Vaucluse, Drôme, Bouches du Rhône, Aix. ITALY : Liguria, Ventimiglia (Fl. It. Exsicc. 643, Fiori, Bég., Pam.), Etruria, Florence, Perugia, Spoleto, Naples ; Sicily. BALKAN PENINSULA : S. Dalmatia ; Ragusa, Gravosa.

Variety β . *TOMENTOSA* Ging. Hist. Nat. Lav. p. 154 (1826) ; Briquet, Lab. Alpes Marit. p. 472 (1895).

This variety is distinguished by its indumentum. This is tomentose on all the leaves and the stems are incanous, farinaceous. Gingins de Lassaraz places var. *tomentosa* as a sub-variety of his var. α *vulgaris* with simple stems. In other respects it is similar to the type. Hab. in France, near Grasse.

L. spica var. *tomentosa* Linn. f. De Lav. p. 154 (1780) is probably a synonym, but the description is inadequate and may refer to *L. lanata* Boiss.

Several other varieties have been described ; these are based on differences in size and shape of leaves and spikes, and partly also on the degree of branching of the peduncles. These characters, which are not very easily defined, are those most affected by hybridization, and this probably accounts for almost all these varieties. Briquet (Lab. Alpes Marit. p. 472 ; 1895) grouped them all together as var. α . *vulgaris*. Rouy and Foucaud (Fl. Fr. xi, p. 256 ; 1909), made var. α . *normalis* and var. β . *erigens*. Jordan and Fourreau (Brev. Pl. Nov. II, pp. 88, 89 ; 1868) described three new species, *L. interrupta*, *L. inclinans*, *L. erigens*. Briquet includes the first two of these in his var. *vulgaris* ; Rouy and Foucaud include the first two in var. *normalis*, the last as a synonym for their var. *erigens*. Hy (in Rev. gén. bot. x, p. 54 ; 1898) considered the three species of Jordan and Fourreau to be of hybrid origin.

This species, *L. latifolia* Vill., is the type of Spike or Spike Lavender of the perfume industry and of gardens, though much cultivated Spike is more or less hybridized with *L. officinalis*.

Synonyms.—*L. Spica* Linn. Sp. Pl. p. 572 (1753) included both *L. officinalis* Chaix (as var. α) and *L. latifolia* Vill. (as var. β). The following are synonyms for *L. Spica* Linn. :—*L. vulgaris* Lam. Fl. Fr. II, p. 403 (1778). *L. fragrans* Salisb. Prodri. p. 78 (1796). *L. Spica* Cav. Descr. p. 69 (1802) ; who quotes Bulliard tab. 337 (1780), but this figure seems to be *L. officinalis* Chaix, and is quoted for *L. Spica* Linn. var. α by Loiseleur (Fl. Gall. II, p. 346 ; 1807).

Two species are now recognized instead of the varieties described by Linnaeus, and much confusion has been caused by the use of the name *L. Spica* Linn. for

both var. α Linn. (true Lavender) and for var. β Linn. (Spike). The name *L. Spica* Linn. has now become completely ambiguous and according to the decision taken at the International Botanical Congress held at Cambridge in 1930 such 'nomina ambigua' should be discarded. The correct name for *L. Spica* var. α Linn. is, then, *L. officinalis* Chaix, and that of *L. Spica* var. β Linn. is *L. latifolia* Vill. (see Kew Bulletin, 1932, p. 295, and 1935, p. 75).

The following are synonyms for *L. officinalis* Chaix in Vill. Hist. Pl. Dauph. I, p. 355 (1786), and II, p. 363 (1787), et auct.:—*L. Spica* Linn. var. α Sp. Pl. p. 572 (1753). *L. spica* L. emend. Loisel. Fl. Gall. II, p. 346 (1807), and numerous authors—with whom it is usually clear from the context whether *L. officinalis* or *L. latifolia* is intended. *L. angustifolia* Mill. Gard. Dict. ed. 8, no. 2 (1768); Moench. Meth. p. 389 (1794); Bubani, Fl. Pyr. I, p. 381 (1897). *L. minor* Garsault, Fig. Pl. Anim. Med. t. 331 (1764), et Deser. Pl. Anim. p. 203 (1767); Thell. in Bull. Herb. Boiss. Sér. II. VIII, p. 792 (1908), who there identifies this as *L. spica* Linn. sensu stricto, excl. var. *L. vera* DC. Fl. Fr. v, p. 398 (1815). *L. pyrenaea* DC. Fl. Fr. v, p. 398 (1815). *L. fragrans* Jord. in Billot, Annot. Fl. Fr. et d'All. p. 171 (1859). Variety:—*L. delphinensis* Jord. in Billot, Annot. Fl. Fr. et d'All. p. 171 (1859). Variety:—*L. leptostachya* Pau in Bol. Soc. Iber. xxvii, p. 171 (1928) (var. or ? hybrid).

And the following are synonyms for *L. latifolia* Vill. Hist. Pl. Dauph. II, p. 363 (1787), et auct.:—*L. Spica* Linn. var. β Sp. Pl. p. 572 (1753). *L. major* Garsault, Fig. Pl. Anim. Med. t. 330 (1764), et Deser. Pl. Anim. p. 203 (1767); Thell. in Bull. Herb. Boiss. Sér. II. VIII, pp. 779, 792 (1908), who there identifies this species as *L. latifolia* Vill. and makes the name *L. major* (Gars.) Thell. *L. Spica* Linn. emend. Chaix in Vill. Hist. Pl. Dauph. I, p. 355 (1786); DC. in Fl. Fr. vi, p. 397 (1815); Loisel. Fl. Gall. ed. 2, II, p. 19 (1828), and numerous authors, with whom it is usually clear from the context whether *L. officinalis* or *L. latifolia* is intended. *L. latifolia* Medic. Beob. p. 135 (1783). *L. latifolia* Desf. Cat. Hort. Paris, ed. 3, p. 395 (1829), quoted as a synonym for *L. ovata* Steud. (Nom. ed. 2, II, p. 17; 1841: ? a variety or hybrid, though description very meagre). *L. erigens* Jord. & Fourr. Brev. Pl. Nov. fasc. 2, p. 88 (1868), having the spike compact; bracts longer than the calyx:—*L. inclinans* Jord. & Fourr. loc. cit.: having the spike interrupted, lax; bracts much longer than calyx. *L. interrupta* Jord. & Fourr. loc. cit.: having the spike much interrupted; bracts longer than calyx. These last three differ as indicated from *L. latifolia* proper, and are either varieties or the result of a cross with *L. officinalis* at some point in their ancestry.

7. *L. LANATA* Boiss. Elench. p. 72 (1838).

Leaves up to 5·5 cm. long, 1·2 cm. broad, linear-ob lanceolate, narrowly spatulate, ob lanceolate or narrowly elliptic, attenuated below; margins slightly revolute; indumentum very dense, white tomentose with long branching hairs. *Peduncles* often branching, sparsely short white tomentose or hispid.

Spike interrupted, lax, sometimes very long, reaching 12 cm. *Bracts* linear to lanceolate; *bracteoles* small, linear to linear-lanceolate, brown, scarious, up to 5 mm. long. *Calyx* 8-nerved, margin with four teeth alternating with four rounded lobes, the posterior lobe enlarged into an upright elliptic slightly cucullate appendage. *Corolla* rather small: tube exceeds calyx by about 3 mm. *Nucule* narrowly oblong, about 2 mm. long: no gelatinous envelope when wet.

Distribution. Europe: mountains up to 6500 ft. S. SPAIN: Andalousia, Jaen, Sierra de la Nieva (*Barbey* 533, *Reverchon* 436), Sierra de la Malessa, Grenada, Sierra Nevada (*Boissier*, *Elenchus*, 155, *Huter*, *Porta & Rigo* 480, 675, *Bourgeau* 1406, *Willkomm* 294).

Synonyms.—? *L. Spica* DC. $\beta.$ *lanigera* Webb, Iter. Hisp. p. 19 (1838) see Colmeiro, Pl. Hisp. Lusit. IV, p. 289; 1888. Webb says that 'this variety is remarkable for its broad leaves thickly beset with white downy wool, but does not otherwise differ from the true *L. Spica*' : but this is not altogether true of *L. lanata*, which differs from *L. Spica* DC. (*L. officinalis* Chaix) also in spike and calyx characters. Var. $\beta.$ *lanigera* Webb, is probably *L. lanata*. *L. tomentosa* Pau, Nuev. Cont. Fl. Grenada, p. 60 (1922).

L. spica var. *tomentosa* Linn. f., De Lav. p. 154 (1780), may refer to *L. lanata* or to *L. latifolia* Vill. var. *tomentosa* Briquet. The description is inadequate. Linnaeus does not mention any type corresponding to *L. lanata*. Gingins de Lassaraz (op. cit. p. 154; 1826) quotes a variety of Tournefort's (Inst. I, p. 198) which is probably *L. lanata* Boiss. Tournefort says 'Lavandula latifolia Hispanica, tomentosa'.

HYBRIDS OF SECTION SPICA.

Hybridization is recorded between species within the section *Spica* and between species of this section and of the section *Stoechas*. The hybrids of *L. officinalis* and *L. latifolia* with *L. dentata* and *L. pedunculata* are considered under section *Stoechas* (p. 170) as *L. heterophylla* Poir., *L. Allardi* Hy, and *L. Eliae* Sennen.

Hybrids of *L. officinalis* and its varieties with *L. latifolia* are numerous, both in natural habitats and in cultivation, and show a large range of intermediates between the parent species. In many of the hybrids, characters of *L. officinalis* seem to predominate, but other hybrids approach *L. latifolia* more nearly. Hy in a paper on Lavenders cultivated in gardens (in Rev. gén. bot. p. 49, 1898) suggested that almost all the cultivated and many of the wild forms which have been described as varieties of *L. officinalis* or *L. latifolia*, or as species other than these, are in reality hybrids. Briquet (in Lab. Alpes Marit. p. 468; 1895) took the opposite view to Hy and included many forms which were originally described as hybrids or new species as simple synonyms of *L. officinalis* or *L. latifolia*, and he recognised only one hybrid, *L. Burnati*, collected and described by himself. I have examined specimens of most of the controversial forms; they almost all show a mixture of the characters of

L. officinalis and *L. latifolia*, sometimes those of one, sometimes those of the other predominating, and in my opinion they are most satisfactorily explained as hybrids.

L. OFFICINALIS Chaix \times L. LATIFOLIA Vill.

\times *L. INTERMEDIA* (*Emeric* in litt.) *Loisel.* *Fl. Gall.* 11, p. 19 (1828).

This is described as having branching shoots [? peduncles], linear-lanceolate leaves, subinterrupted spikes, ovate-acuminate nerved bracts, striated tomentose calyces, and blue flowers. Basses Alpes, Forcalquier, coll. *Emeric*.

Loiseleur evidently considered it to be intermediate between *L. officinalis* and *L. latifolia*; his description is not very precise, but may be construed in this light.

\times *L. BURNATI* *Briquet*, *Lab. Alpes Marit.* p. 468 (1895).

Plant reaching 60 cm.; stems robust, branches numerous, greenish, peduncles very long. Leaves linear-oblong, narrow, obtuse, margins slightly convex, revolute, base attenuated, green on both surfaces, $3-5 \times 0.1-0.4$ cm. Spike slender as in *L. latifolia*, \pm interrupted. Bracts lanceolate, enlarged at the base, nearly equal to the calyx, green, nerves intermediate between the parents. Bracteoles linear, green, small, numerous. Calyx-indumentum tomentose-lanuginous, purplish. Flowers as in the parents. Anthers with little, poorly developed pollen. Hab. near Tour de Tinée, between the parents, *Briquet* (10. vii. 1887).

\times *L. SPICA-LATIFOLIA* *Albert* in *Feuilles des jeunes Naturalistes*, vi, p. 38 (1875), et *Bot. du Var*, p. 40 (1884); *L. hybrida* (*Albert* ms., *Reverchon* ms.) *Briquet*, *Lab. Alpes Marit.* p. 468 (1895).

Lower leaves densely white tomentose; bracts membranous, lateral veins conspicuous, the lowest bracts lanceolate, the upper broadly lanceolate or ovate, the apex elongated acute, almost as long as the calyx; bracteoles linear-lanceolate; calyx-indumentum lanuginous-tomentose, grey with purplish tinge; corolla-lobes rather small, approaching *L. latifolia*; spike long, \pm interrupted, robust; peduncles simple or with small branches. *Briquet* (*Lab. Alpes Marit.* p. 468), considered this species to be simply *L. officinalis*, but *Reverchon's* specimens at Kew (from which the above description is taken) show several typical hybrid-characters.

Distribution. S. FRANCE; Vaucluse (Flassau, 17. vii. 1876 et 15. vii. 1877, Mt. Ventoux 17. vii. 1877, *Reverchon*, leg. Autheman), Var, Ampus (Soc. Rochel. 4312), Drôme, Nyone (Soc. Rochel. 4312²).

\times *L. AURIGERANA* *Mailho* in *Bull. Soc. Rochel.* p. 42 (1889), ex *Briquet*, *Lab. Alpes Marit.* iii, p. 468 (1895).

This plant was described as a hybrid between *L. pyrenaica* (= *L. officinalis* var. *pyrenaica*) and *L. latifolia*. *Briquet*, who saw the type-specimen (*Magnier*

exsicc. 3087) considered it to be *L. officinalis*, and Rouy and Foucaud (Fl. Fr. xi, p. 255; 1909) quote it as a synonym for *L. officinalis* var. *delphinensis*. I have also seen the type-specimen, and it differs from *L. officinalis* in its *peduncles* with few slender branches and in the *bracts*, the lower ovate-lanceolate nearly as long as the calyx, the upper ovate, shortly acuminate, about $\frac{2}{3}$ as long as the calyx. It resembles *L. officinalis* in its narrow *leaves* and robust interrupted *spike*; the general *habit* of the plant suggests *L. latifolia*; the short grey tomentose *indumentum* of the *calyx* resembles that of *L. latifolia* or of *L. officinalis* var. *pyrenaica*.

Distribution. Europe. FRANCE: French Pyrenees; Ariège (Arignac, inter parentes, Fl. Sel. exsicc. Magnier 3087), Pyrénées Or., Villefranche (inter parentes, Soc. Rochel. 2688², Sennen).

There are two specimens named *L. aurigerana* (Arignac, Soc. Roch. 2688 *Mailho*); but these differ from *L. latifolia* only in their *peduncles*, which are slightly branched or simple.

×L. SENNENI Foucaud ms. in Herb. Kew., nom. nov.

The plants I have seen at Kew and in Herb. Barbey-Boissier resemble *L. officinalis* var. *delphinensis*, except that the *bracts* of *L. Senneni* are larger than usual and the lowest pair is lanceolate-ovate or long broadly acuminate ovate, nearly equal to the calyx; all the bracts are membranous; the *calyx-indumentum* is short grey tomentose, resembling *L. latifolia* and *L. officinalis* var. *pyrenaica*, and the *peduncles* are usually simple, but may have a pair of small slender branches.

Distribution. Europe. FRANCE: Pyrénées Or. (Villefranche near Belloc Sennen, 22. vii. 1897, Herb. Kew.), Villefranche-de-Conflet, Belloc and Conat (Soc. Rochel. 4140 Sennen).

×L. HORTENSIS Hy in Rev. gén. bot. x, p. 49 (1898).

Cultivated. *L. latifolia* × *officinalis*. This hybrid resembles *L. latifolia* in *habit* and branching *peduncles*, and in slender interrupted *spikes*. The primary *leaves* of the young shoots are very large (9·5×1 cm.), linear-elliptic, glabrescent, the base attenuated, having ± fastigiate and ± tomentose linear leaves in their axils. The lower *bracts* are green, lanceolate, the base dilated, the upper ovate ± acuminate, brown tinged with purple or blue; all bracts have conspicuous lateral nerves. The *calyx-indumentum* is lanuginous-tomentose, grey or purplish.

Distribution. Frequent in gardens of W. FRANCE. Cult. Angers (Soc. ét. fl. Franco-helv. 788 *Hy*; Soc. Rochel. *Hy*).

×L. FERAUDI Hy in Rev. gén. bot. x, p. 55 (1898).

This hybrid is described as differing from *L. latifolia* Vill. as follows:—'Feuilles des rameaux stériles étroites.' In herb. Feraudi.

Distribution. FRANCE: Carpentras.

\times L. GUILLONI *Hy* in Rev. gén. bot. x, p. 55 (1898).

This hybrid is described as differing from *L. latifolia* Vill. as follows:—
'Thyrse simple ou à rameaux très courts.' (Soc. Dauphin. no. 1326 bis.)

\times L. LEPTOSTACHYA *Pau* in Bol. Soc. Iber. xxvii, p. 171 (1928).

Described as a new hybrid, the *bracts* similar to *L. officinalis* var. *pyrenaica*, from which it differs in its slender *spikes*, approaching those of *L. latifolia*, with few lax flowers; nerves of *bracts* not or only occasionally branched in the upper regions; *bracts* narrower.

Distribution. SPAIN.

There is a specimen from Italy, E. Calabria, Mt. Pollino (8–900 m. *Huter, Porta and Rigo* 451), which is probably a hybrid of *L. officinalis* var. *angustifolia* with *L. latifolia*. The plant is small, about 25 cm. high, the *leaves* all tomentose, linear to linear-lanceolate, acute, margins much revolute; the *peduncles* unbranched, grey-tomentose; the lower *bracts* herbaceous, lanceolate or ovate-lanceolate, longer than the calyx, the upper ovate acute, about $\frac{2}{3}$ of the length of the calyx. The *calyx* is large, 6·5 mm. long, the marginal teeth and *corolla* also large.

SECTION III. PTEROSTOECHAS *Ging.* Hist. Nat. Lav. pp. 120, 158 (1826);
Benth. Lab. i, p. 149 (1833).

Original diagnosis, Ging. op. cit. p. 158. 'Charact. Flores spicati spica tetragona, bracteis unifloris, coma nulla.'

Observ. Caryopsides ovatae extus ad basin areola umbilicali magna obcordata notatae, squamae gynobaseos maxima caryopsidibus totae adhaerentes, calyx sub-bilabiatus 3/2 dente medio labii superioris latoire non appendiculato. Herbae perennes aut basi tantum lignosae.'

The habit of species of the section *Pterostoechas* is herbaceous or suffruticose, the *stems* much branched, often slightly woody at the base. The *leaves* are usually pinnate or bipinnate; they may be dentate to laciniate-dentate (*L. rotundifolia*) or entire (*L. atriplicifolia*). The *spike* is lax or compact, quadrate, cylindrical or flattened biseriate; the *bracts* are all fertile, each supporting a single flower, the uppermost not sterile enlarged comose. *Bracteoles* are absent. The *calyx* is sessile, 5-lobed, \pm bilabiate 3/2, the median posterior tooth usually broader than the others, not appendiculate. The *calyx* is 15-nerved; both Gingins de Lassaraz and Bentham describe it as 13-nerved, but I have examined specimens of each species and found them all to be 15-nerved. Sometimes one or two nerves fork about 0·5 mm. above the base, so that the *calyx* is 13-nerved quite at the base, but the major portion is always 15-nerved. The *corolla*-tube is considerably longer than the *calyx*, sometimes more than double its length; the *corolla*-lobes are usually bilabiate, 2/3, the posterior lobes erect, much larger than the spreading anterior lobes, or they may be of almost uniform size (*L. atriplicifolia*, *L. rotundifolia*). The *nucules* are oblong to obovate or rotund oblong; the *areoles* white, rotund-obovate or oblate, $\frac{1}{2}$ to $\frac{1}{3}$ length

of nucule; when soaked in water the nucules sometimes show a mucilaginous coat of varying thickness.

Distribution. Representatives of section *Pterostoechas* occur in the Mediterranean regions excluding the Balkans and Asia Minor, in Northern Tropical Africa from Somaliland to Nigeria, and in the Tropical and Temperate Atlantic Islands. There is a tendency for allied species to occur in widely separated areas with a chain of related species in the intervening regions. The species of this section seem to be rather in the course of segregation than to have reached stability, and the exact delimitation of any one species is often difficult to define.

KEY TO THE SPECIES OF SECTION PTEROSTOECHAS.

1. Leaves \pm dissected; corolla \pm bilabiate 2/3, the lobes broad rotund ovate or oblong, rounded.
 2. Leaves deeply divided, pinnate-dentate, pinnate or bipinnate.
 3. Leaves irregularly pinnate-dentate, pinnate or bi-pinnate, not pectinate-pinnate.
 4. Indumentum not incanous; leaves smaller (usually \pm 3–6 cm.), segments broadest at the base, or linear.
 5. Plants bushy, the stems branching, becoming slightly thickened and somewhat woody with age; leaf-segments narrow.
 6. Stem with long grey villous indumentum; calyx and sometimes bract white tomentose-lanuginous... 8. *L. multifida*.
 - 6*. Stems glabrous or with pubescent, tomentose, or hirsute indumentum; inflorescence parts not tomentose lanuginous.
 7. Bracts large ovate-lanceolate concealing calyx; typically herbaceous 9. *L. Mairei*.
 - 7*. Bracts small, scarcely exceeding the calyx in length and often much shorter, never concealing the calyx entirely, scarious.
 8. Calyx bilabiate, the teeth heteromorphous; leaf-segments oblong to ovate.
 9. Three teeth of posterior labium of calyx very short-deltoid, almost uniform, strongly bilabiate.
 10. Spikes short (3–4 cm.) stout, sometimes ternately branched; bracts about half calyx-length, as broad or broader than long 10. *L. maroccana*.
 - 10*. Spikes long (up to 8 cm.) slender, peduncle and base of spike much branched; bracts equal to calyx-length or longer, ovate or lanceolate..... 11. *L. canariensis*.
 - 9*. Three teeth of posterior labium of calyx broadly ovate to lanceolate, the median tooth the broadest, somewhat bilabiate. The following four species and *L. maroccana* above are closely allied and might be considered as subspecies of *L. pubescens* Dene.

11. Corolla-tube dilated immediately above calyx-margin, below the insertion of the stamens 12. *L. Antineae.*

11*. Corolla-tube dilated at or above insertion of stamens.

12. Bracts $\frac{1}{2}$ to $\frac{1}{3}$ calyx-length (at flowering stage) 13. *L. brevidens.*

12*. Bracts $\frac{2}{3}$ calyx-length or more (at flowering stage).

13. Peduncle and spike simple; stem and leaf indumentum sparse, hispid or pubescent 14. *L. tenuisecta.*

13*. Peduncle and base of spike usually much branched; indumentum of stem and leaf dense, hirsute hispid or pubescent 15. *L. pubescens.*

8*. Calyx-teeth subhomomorphous, the median posterior tooth slightly broader than the other 4 uniform teeth; leaf-segments very narrow, linear 16. *L. stricta.*

5*. Main stem short, much thickened, woody, crowned with young ascending shoots arising amongst the broken bases of previous shoots; leaf-segments broad, ovate to oblong 17. *L. somaliensis.*

4*. Indumentum of whole plant incanous, of very short, dense, grey hairs; leaves large up to 8.5 cm. segments broadest at the apex, or linear 18. *L. pinnata.*

3*. Leaves very regularly pectinate-pinnate or pectinate-dentate.

14. Leaves up to 8 cm. long and 4 cm. broad, segments broad, rachis winged. Indumentum hirsute-pubescent 19. *L. foliosa.*

14*. Leaves up to 4.5 cm. long and 2 cm. broad, segments narrow, rachis not winged. Indumentum floccose-tomentose 20. *L. Minutolii.*

2*. Leaves rotund or \pm triangular, margins dentato to laciniately dentate 21. *L. rotundifolia.*

1*. Leaves entire; corolla almost regular, the lobes narrow, linear-lanceolate, acute 22. *L. atriplicifolia.*

DISCUSSION OF THE SECTION PTEROSTOECHAS.

8. *L. MULTIFIDA* Linn. Sp. Pl. p. 572 (1753).

Leaves ovate to rotund-ovate in outline, up to 3.5 cm. long including petiole of 3–6 mm., bipinnate or pinnate, the segments \pm deeply dentate: segments or teeth subcuneate, ovate, lanceolate to almost linear, their margins entire, and apex acute. *Indumentum* of leaves villous to shortly hispid; of young stems \pm densely short grey tomentose with branched hairs, intermixed with \pm numerous unbranched long grey hairs. *Peduncles* slightly villous and \pm densely short grey tomentose becoming lanuginous below the inflorescence. *Spike* simple or ternately branched, two shortly pedunculate spikes arising at the base of the median one; spike compact or occasionally interrupted,

usually rather short and thick, though it may reach 7·5 cm. in fruiting stage. *Bracts* arranged in alternating pairs, forming four \pm vertical tiers each an open spiral on the axis ; bracts obovate-elliptic, base truncate, apex sharply acute, three dark main nerves very typical ; median portion scarios, wings membranous ; equal to length of calyx or slightly shorter ; tomentose to hirsute, hairs grey, branching. *Calyx* 5·5 mm. long, ovate-cylindrical, base inflated in fruiting stage ; \pm densely white tomentose, especially on the margins and nerves ; 15-nerved ; bilabiate 3/2, the anterior teeth lanceolate, \pm reflexed when nucules are ripe, the posterior deltoid. *Corolla*-tube nearly double the calyx-length ; lobes large, the posterior pair 3·5 mm. long. *Nucules* 2 mm. long, obovate-elliptic, minutely verruculose, purplish brown, slight gelatinous coat when wet ; areole triangular, \pm $\frac{1}{2}$ length of nucule.

Distribution. Europe. PORTUGAL (*Welwitsch* 193). S. SPAIN (*Bourgeau* 813, 1404; *Reverchon* 508; *Porta and Rigo* 31), Gibraltar (*Willkomm* 680). ITALY : Calabria (Capo del Armi, *Huter, Porta & Rigo* 228, *Lacaïta* 156/20).

N. Africa. TUNIS : Sousse, Gabes (*Kralik* 347). ALGERIA : Oran, Alger, Biskra (*Munby* 48; *Frag. Fl. Alg.* *Schmitt* 78; *Chevallier* 469; *Balansa* 442, 836; *Jamin* 197; *Soc. Fr. exsicc.* *Duffour* 1007; *Battandier & Trabut* 177). MOROCCO, NW. and SW. regions, Anti-Atlas (*Hooker, Agadir, Tangier and Tetuan, and S. Morocco* 1871; *Mission Sci. Soc. Géogr. Maroc. Pitard* 1647, et *Rabat* 2332; *Quer* 525). UPPER EGYPT (*Frigari, Parlatoore*, 1847).

NW. Tropical Africa : MAURITANIA : St. Louis (Herb. Pomel. Univ. Alger).

Synonym.—*L. pinnatifida* (Linn.) Webb, *Iter Hisp.* p. 19 (1838), who gives no description, and I can find no *L. pinnatifida* Linn., though Webb quotes 'Linn.' as the authority. The plant collected in Spain and Portugal can only have been *L. multifida*.

L. multifida is diagnosed especially by its long villous stem-indumentum, \pm grey tomentose bracts and calyx, and by the conformation of the spike.

9. L. MAIREI *Humbert* in *Bull. Soc. Hist. Nat. Afr. Nord.*, xviii, p. 157 (1927).

Stems suffruticose below, 20–30 cm. high ; branches spreading, \pm ascending. *Leaves* ovate or lanceolate in outline, usually small, up to 2·5 cm. long including petiole 3–7 mm., about 1 cm. broad, leaves of lower nodes on main stems larger, up to 4 cm. long ; irregularly bipinnate ; segments few (3–6) on each side, remote, oblong, ovate or obovate, obtuse, the margins plane or slightly revolute. *Indumentum* of stems and leaves uniformly grey-puberulous or hispid, very sticky, the non-glandular hairs short and rather dense and often branched, the glands numerous, subsessile or stipitate. *Spikes* and *peduncles* unbranched, or peduncle ternate at the base. Spike compact, occasionally interrupted, 1·5–4 cm. long, cylindrical or \pm quadrate. *Bracts* arranged in opposite pairs, \pm imbricate or 4-tiered, herbaceous, large, 5–7·5 mm. long, 2·5–4 mm. broad, ovate-lanceolate, concealing calyx, margin entire or slightly 1–2-dentate ; nerves 3 at the base, the outer pair branching to form 5 main nerves ; indumentum pubescent of fine branching hairs. *Calyx* cylindrical-urceolate,

about 5 mm. long, slightly dilated below; bilabiate, the median posterior tooth broadly triangular, 0·5 mm. broad, 0·25 mm. long, the lateral pair slightly longer; 2 anterior teeth lanceolate, about 1·5 mm. long, spreading in mature fruit; nerves 15, prominent; indumentum pubescent, margins shortly ciliate. *Corolla* deep violet, 12–16 mm. long, externally puberulous, the throat and interior of the tube below the stamen-insertion villous. *Nucules* elliptic-obovate, 1·5 mm. long, dark, minutely muricate; areole obovate-cordate, $\pm \frac{1}{3}$ nucule length.

Distribution. North Africa. MOROCCO: SE. deserts, Great Atlas, Anti-Atlas, on calcareous soil (*Humbert* 413, 495, 1832; *Maire*).

L. Mairei is allied to *L. multifida* Linn., from which it is distinguished by its large bracts and hirsute or pubescent (not long-villous) stem-indumentum.

Varieties.

β . *INTERMEDIA* *Maire* in Bull. Soc. Hist. Nat. Afr. Nord, xxiv, p. 223 (1933). The variety differs from the type in its greater height, up to 50 cm. more or less, in the larger *peduncles* and *spikes* (the latter up to 7 cm. long). The *indumentum* is less dense, not \pm grey when dried. The *bracts* are larger than those of the type, about 8 mm. long, ovate, greenish or scarious, the nerves dark. *Calyx-indumentum* short sparse pubescent.

Distribution. N. AFRICA. MOROCCO: Anti-Atlas, high calcareous ground, 1000–1300 m. (*Arganias*, *Maire*; *Tifernin*, Soc. Fr. exsicc. Duffour 6969, *Maire*).

γ . *ANTIATLANTICA* *Maire* in Bull. Soc. Hist. Nat. Afr. Nord, xxiv, p. 223 (1933).

L. antiatlantica *Maire*, loc. cit. xx, p. 194 (1929).

Var. *antiatlantica* is distinguished from the type and from var. *intermedia* by its greater size, for it is up to 1·25 m. high, and by the *stem indumentum* of sparse hairs over numerous very short glandular hairs, and by the *bracts*. These are membranous, lanceolate, 5·5–8 mm. long, the apex cuspidate recurved, nerves slightly dark. *Corolla* deep violet-blue, \pm 14 mm. long, lobes rather larger than those of the type.

Distribution. North Africa. MOROCCO: Anti-Atlas (*Adar-ou-Aman*, *Maire*; Dj. Tourgueth, *Ibrahim*).

This variety was described as a species by Dr. *Maire* in 1929, after the publication (1927) of the description and name *L. Mairei* *Humb.*, though *L. antiatlantica* was actually discovered earlier. The discovery of *L. Mairei* var. *intermedia* *Maire* made a connecting-link between *L. Mairei* and *L. antiatlantica*; and Dr. *Maire* then reduced his species to a variety of *L. Mairei* *Humb.*

10. *L. MAROCCANA* *Murb.* in Bot. Not. p. 269 (1922), et Contr. Fl. Maroc. II, p. 25 (1923).

Stems ascending or erect, 6–12 dm. high, base suffruticose, internodes usually much elongated, with few leaves; glabrescent or sparsely pubescent. *Leaves*

lanceolate or ovate in outline, up to 4 cm. long (including petiole up to 1 cm.) and 25 mm. broad, pinnate or bipinnately lobed, the segments distant not decurrent on the rachis or scarcely so, the lower 2-3-lobed, the upper usually entire; segments all oblong or oblong-linear. *Indumentum* of leaves very short, sparsely aspros-puberulent of hooked hairs with scattered pedicellate glands. *Peduncles* often branched; *spikes* usually simple, \pm regularly quadrate, compact, those of main axis 3-4 cm. long, of lateral branches about 1-1.5 cm. long, oblong or elliptic-ovate. *Bracts* 2.5-3.5 mm. long, about one-half as long as the calyx, orbicular-pentagonal, with the upper margin slightly broader than the whole length of the bract, apiculate, shortly puberulent, membranous, pale grey, the nerves 5 (outer pairs anastomosing at the base) blue-purple. *Calyx* ovate-oblong, base dilated in fruit, 5-6 mm. long, 15-nerved, the nerves and teeth blue-purple; bilabiate $3/2$, the three posterior teeth broadly deltoid, obtuse, twice or thrice as broad as long, the anterior pair narrowly lanceolate, acute, erect (not deflexed in fruit), about 1 mm. long. *Corolla* about 14 mm. long, violet-blue, the upper lobes much larger than the lower. *Nucule* rotund oblong, 1.5 mm. long, 1 mm. broad; areole cordate-orbicular, $\frac{1}{3}$ nucule length.

Distribution. North Africa. S. MOROCCO: Great Atlas and Anti-Atlas Mts., W. Coastal region (Ait Mesan, *Ball*, It. Maroc. 1871, May 13-16; Dj. Hadid and Gt. Atlas, *Hooker*, 1871); Dj. Hadid, *Ibrahim* ex herb. Cosson; Tagadirt, *Murbeck* It. 1921; Backhoum, Agadir-n-Ighir, Ida-ou-Tanar *Maire*; *Jahandiez* 274 bis, Oued Tssen, 738 Reraya).

Synonyms.—See under *L. tenuisecta* Coss. for discussion of these. *L. abrotanoides* var. *attenuata* Ball in *Journ. Bot.* 1875, p. 175. *L. tenuisecta* (Coss.) Ball in *Journ. Linn. Soc. Lond.*, Bot. xvi, p. 609 (1878), pro parte.

L. maroccana Murb. is closely allied to *L. tenuisecta* Coss., and was not distinguished from it by the earlier authors (Ball, loc. cit.; see under *L. tenuisecta* Coss.). *L. maroccana* differs from *L. tenuisecta* in its more sparse stem-indumentum and in its denser, more regularly quadrate inflorescence. The bracts of *L. maroccana* are very broad, sharply apiculate, $\frac{1}{2}$ (not $\frac{2}{3}$) of the length of the calyx; the calyx is rather larger and the posterior teeth uniform and broader than those of *L. tenuisecta*; both bract and calyx are pale greyish in colour, the nerves and apices purplish blue. The corolla-lobes are rather larger and the nucule more rotund than those of *L. tenuisecta*.

11. *L. CANARIENSIS* Mill. *Gard. Dict.* ed. 8, no. 4 (1768).

Leaves lanceolate or ovate in outline, pinnate or \pm bipinnate; segments entire, narrow, linear to oblong, obtuse or rounded. *Indumentum* short, stiff, hispid, with rather longer branching hairs more dense on the leaves than on the stems; nodes \pm tomentose when young. *Peduncles* usually very long, up to 30 cm., branching. Base of *spike* commonly branched; spike slender, cylindrical, up to 10 cm. long. *Bracts* arranged in alternating pairs, lanceolate or ovate, acute to acuminate, 5 main veins, usually blue especially in young inflorescences; hirsute or almost glabrous, slightly longer than the calyx in

flowering state. *Calyx* 3·5-4 mm. long, 15-nerved, \pm bilabiate; posterior teeth cuneate; anterior teeth ovate or lanceolate, reflexed in fruit. *Corolla*-tube more than double the calyx-length, externally pubescent. *Nucules* oblong, 1·25 mm. long, pale brown; areole small, rotund.

Distribution. Atlantic Islands. CANARIES: Teneriffe (Webb, Berthelot, Lowe G 41, Bourgeau 904, 1476), Palma, Grand Canary (Murray), Gomera, Hierro.

Synonyms.—*L. abrotanoides* Lam. Encycl. meth. III, p. 429 (1791); Willd. Sp. Pl. ed. Willd. III, p. 62 (1801). *L. elegans* Desf. Tabl. ed. i, p. 59 (1804). *Stoechas abrotanoides* Reichb. f. in Oestr. Bot. Wochenbl. VII, p. 161 (1857). *L. multifida* subsp. *canariensis* (Mill.) Pitard & Proust, Fl. Canar. p. 299 (1908).

L. canariensis shows affinities with *L. multifida* Linn. and with *L. pubescens* Dene. and the allied group of species. It may be distinguished from *L. multifida* by the indumentum, strongly hispid or \pm tomentose, not long grey villous on the stems, by the much branched inflorescence, long slender spikes tinged with blue but not lanuginous, and by the coloured prominent nerves of the bracts. *L. abrotanoides* differs from *L. pubescens* in stem-indumentum, hispid or \pm tomentose of branching hairs, in leaf-shape, the segments linear, scarcely decurrent, rather regular, in the blue coloration of the bracts and calyces, and in the longer corolla-tube and much larger lobes.

Bentham (Labiatae Gen. et Sp. I, p. 150; 1833) mentions cultivated specimens from Mexico and Montpellier, now in the Kew Herbarium, remarkable for the very narrow acute segments of the leaves, which are often pinnate (not bipinnate as is usual), and for the densely hirsute bases of the stems of the Montpellier specimen. He decided that these examples were better considered as cultivated varieties than as constituting separate species, and indeed the leaf-shape and indumentum fluctuate considerably in the wild plant.

12. L. ANTINEAE Maire in Bull. Soc. Hist. Nat. Afr. Nord, xx, p. 32 (1929).

Stems suffruticose, 6-8 dm. high. *Leaves* small, rotund-ovate to lanceolate in outline, about 3 cm. long and 2 cm. broad, pinnate; segments entire or the lower ones lobed, linear or lanceolate-linear or linear-ob lanceolate, obtuse, \pm decurrent on the narrowly winged rachis, margins \pm revolute. *Indumentum* of young stems grey-puberulous of short jointed branched hairs, and very shortly pubescent; older stems and peduncles glabrescent; leaves hispid or pubescent, with short stiff \pm branched hairs. *Spikes* and *peduncles* often much branched, sometimes simple; spike cylindrical, fairly compact, up to 8·5 cm. long. *Bracts* 3-3·5 mm. long, $\frac{1}{2}$ to $\frac{2}{3}$ calyx-length, broadly ovate, ovate-lanceolate or rotund, apiculate, the lower bracts sharply, the upper gradually acuminate; nerves 3, confluent at the apex, the outer pair 1-3-branched. *Calyx* cylindrical, \pm inflated in the fruiting stage, 5-5·5 mm. long, \pm bilabiate, 3/2; anterior teeth laciniate-lanceolate, 1·5-1·7 mm. long; the posterior three vary (see under forms), margins ciliate. *Corolla* vivid blue, about 15 mm. long, tube much dilated immediately on leaving calyx (below stamen insertion); posterior

lobes obovate about 3 mm. long, \pm recurved; anterior short about 1.5 mm. spreading, ovate-rotund. *Nucules* 1.75 mm. long, oblong-elliptic, slightly rough; areole rotund.

Distribution. NW. Tropical Africa. CENTRAL SAHARA: Ahaggar. FRENCH NIGERIA: Air (Herb. Chevalier 43401).

Forms: *typica* Maire in Bull. Soc. Hist. Nat. Afr. Nord, xx, p. 33 (1929). Median posterior calyx-tooth ovate-triangular, 0.7–0.8×0.7 mm., posterior lateral teeth ovate-lanceolate. SAHARA: Ahaggar (*Maire* 939, 941).

platynota Maire, loc. cit. Median posterior calyx-tooth triangular, broader than long, 0.5×1.0 mm., lateral posterior pair triangular. SAHARA, Ahaggar (*Maire* 931, 932, 934, 942, et Soc. Cénom. d'exc. 2231, *Maire*).

stenonota Maire, loc. cit. Median posterior calyx-tooth ovate-lanceolate, longer than broad, 1.3×0.7 mm., rather long-acuminate, lateral posterior teeth lanceolate. SAHARA: Tefedest, Ahetes (*Maire* 936).

L. Antineae is very nearly allied to *L. brevidens* Maire, from which *L. Antineae* differs in the more compact, rarely interrupted spikes, more divided leaves, elliptic-oblong slightly verruculose nucules, rotund areoles, and especially in its larger corolla, the tube much dilated even below the stamen-insertion. *L. Antineae* resembles *L. stricta* Del. (*L. coronopifolia* Poir.), but is distinguished from the latter by the more compact spikes, longer broadly ovate imbricate bracts, the vivid blue (not pale blue) much larger corolla with more dilated throat, and by the heteromorphic, not sub-homomorphic calyx-teeth.

13. *L. BREVIDENS* (*Humbert*) *Maire* in Bull. Soc. Hist. Nat. Afr. Nord, xx, p. 33 (1929).

Leaves ovate or oblong in outline, up to 2.5 cm. long including petiole up to 5 mm., pinnate, segments entire or lobed, oblong-linear to linear-ob lanceolate, obtuse. *Indumentum* hispid, pubescent, sometimes glandular. *Peduncle* and base of *spike* sometimes branched; spike usually 3–4 cm. up to 9 cm. long, slender, rather lax, base \pm interrupted. *Bracts* ovate-rotund to ovate, $\frac{1}{2}$ to $\frac{3}{4}$ calyx-length; nerves 3, dark, prominent, concurrent at the apex; central portion pubescent scarious; margins glabrescent. *Calyx* 4.5–5 mm. long, slightly pubescent, interior of teeth ciliate, slightly bilabiate; median posterior tooth triangular as long as broad or broader than long; lateral-posterior teeth ovate-triangular; anterior pair lanceolate. *Corolla* intensely violet, retrorse villous below insertion of the stamens, about 10 mm. long, exterior shortly pubescent, bilabiate, the posterior labium about 1.5 mm. long. *Nucules* elliptic-obovate, smooth.

Synonym.—*L. coronopifolia* Poir. subsp. *brevidens* Humbert in Bull. Soc. Hist. Nat. Afr. Nord, xviii, p. 155 (1927).

Varieties.

α. *ZIZIANA* (*Humbert*, loc. cit.) *Maire*, loc. cit.

Stems hispid, glandular, the long hairs (up to 1 mm.) simple, the short hairs simple or with retrorse spiny branches; glands pedicellate. *Leaves* ovate in

outline, 8–20 mm. long including petiole 1–3 mm., pinnate, segments all simple or the lower ones lobed, very glandular and minutely hairy on both surfaces. *Bracts* 2 mm. long, about $\frac{1}{3}$ calyx-length, ovate-rotund, apiculate. *Calyx* 4·5–5 mm. long; median posterior calyx-tooth as long as broad, about $\frac{1}{8}$ calyx-length.

Distribution. N. Africa. SE. MOROCCO : Mt. Bou, Hamid, Wadi Ziz near Rich (*Humbert* no. 1847).

β. MOULOUYANA (*Humbert*, loc. cit. p. 156) *Maire*, loc. cit.

Stems with short simple or retrorse spiny branched hairs, long hairs absent; non-glandular. *Leaves* oblong in outline about 30 mm. long including petiole about 5 mm., pinnate, segments entire or with one or two lobes, minutely hispid and very sparsely glandular on both sides. *Bracts* 2–2·5 mm. long, scarcely $\frac{1}{2}$ calyx-length, broadly ovate, shortly acuminate. *Calyx* about 5 mm. long, the median posterior calyx-tooth slightly broader than long, about $\frac{1}{8}$ calyx-length.

Distribution. N. Africa. E. MOROCCO : Upper Moulouya near Midelt (*Humbert* 950).

γ. MESATLANTICA (*Humbert*, loc. cit.) *Maire*, loc. cit.

Stems hispid and sparsely glandular (as var. *ziziana*) below, pubescent and scarcely glandular above. *Leaves* oblong in outline, 15–23 mm. long including petiole 3–4 mm., pinnate; segments with one or more lateral lobes, hispid and very sparsely glandular. *Bracts* about $\frac{1}{2}$ calyx-length, 2·5–3 mm., ovate, acute. *Calyx* 5 mm. long, median posterior calyx-tooth almost twice as broad as long, about $\frac{1}{8}$ calyx-length.

Distribution. N. Africa. E. MOROCCO : Mid-Atlas and Moulouya (*Humbert* 810, Mt. Larais, Talialit).

L. brevidens is allied in many respects to *L. stricta* Del., *L. tenuisecta* Coss., and *L. Antineae* Maire. The points of difference between *L. brevidens* and *L. Antineae* are considered in the notes on *L. Antineae* (see p. 187). *L. brevidens* differs from *L. stricta* in its more dense, imbricate spikes and heteromorphous calyx-teeth, and to some extent in leaf- and bract-shape. It is distinguished from *L. tenuisecta* by the difference in size of bract (those of *L. tenuisecta* are approximately equal to the calyx) and by the calyx-teeth, the median posterior tooth of *L. tenuisecta* being broader and shorter. The leaf-segments of *L. tenuisecta* are usually broader than those of *L. brevidens*.

The var. *mesatlantica* most resembles both *L. stricta* and *L. tenuisecta*.

14. *L. TENUISECTA* Coss. in Bull. Soc. Bot. Fr. xxii, p. 65 (1875), name only; Ball in Journ. Linn. Soc. Lond., Bot. xvi, p. 609 (1878), pro parte.

Leaves ovate in outline, up to 3·5 cm. long, but usually smaller, shortly petiolate, pinnate or \pm bipinnate; segments linear-oblong, narrowly elliptic or oblanceolate-elliptic, \pm decurrent on the narrowly winged rachis; apex acute or rounded; margins slightly revolute. *Indumentum* of stems very short,

pubescent, interspersed with longer scattered hairs; that of leaves hispid, with short stiff \pm hooked hairs. *Peduncles* simple or branched at the base; *spikes* simple, base usually interrupted, rather lax, cylindrical, short at flowering stage, elongating up to 10 cm. in fruit. *Bracts* scarious, 3–4 mm. long, about $\frac{2}{3}$ calyx-length, lanceolate, ovate or obovate-elliptic, apex gradually or \pm abruptly shortly acuminate; of the three principal nerves the outer pair branched, all prominent, rather dark brown. *Calyx* cylindrical, base slightly inflated in fruit, 4–5 mm. long, pubescent, 15-nerved, slightly bilabiate, 3/2; median posterior tooth twice as broad as long; lateral pair narrower, triangular, acute; anterior teeth lanceolate, about 1.5 mm. long, slightly recurved in fruit, margins ciliate. *Corolla*-tube only slightly dilated, about double calyx-length; lobes rather small. *Nucules* oblong, 1.75 mm. long; areole obocordate, pale greenish brown.

Distribution. N. Africa. MOROCCO: (Djebel Ouensa, Dj. Touchka, Dj. Afougeur, Ibrahim ex herb. Cosson; Dj. Afougeur, *Kralik & Cosson*, leg. Ibrahim, Soc. Dauph. no. 1785), Grand Atlas, Ourika (Mentaga Maire).

The name *L. tenuisecta* was published by Cosson (loc. cit. above) in 1875 in a list of plants from Morocco, but he never published a description. Ball in 1878 (loc. cit. above) published a description of '*L. tenuisecta* Coss. MSS.' which he identified with *L. abrotanoides* var. *attenuata* described by him in the 'Journal of Botany', XIII, p. 174 (1875), quoting the type-specimens of Cosson and that of his var. *attenuata*. These specimens are now at Kew. The type of var. *attenuata* Ball corresponds exactly with *L. maroccana* Murb., and Ball's description for '*L. tenuisecta* Coss. MSS.' covers this species and *L. tenuisecta* Coss., sensu stricto. The description above is based on Cosson's type-material and other specimens in the Kew Herbarium.

L. tenuisecta Coss., sensu stricto, shows affinities with a number of species, including *L. pubescens* DCne., *L. brevidens* var. *mesallantica* (Humbert) Maire, and *L. maroccana* Murb. The diagnostic features are considered in the notes on these species.

15. *L. PUBESCENS* Decaisne in Ann. Scî. Nat. sér. 2, II, p. 246 (1834).

Leaves ovate-rotund to oblong-lanceolate in outline, up to 4 cm. long including petiole up to 1 cm., \pm bipinnate, segments oblong to cuneate, decurrent; apex acute to rounded; margins sometimes revolute. *Indumentum* of stems and peduncles hirsute and minutely pubescent; that of leaves pubescent to densely hirsute. Inflorescence, *peduncles* and base of *spike* typically much branched, spikes \pm quadrate-cylindrical, usually 2–6 cm. long, elongating to as much as 18 cm. in fruit. *Bracts* arranged in alternating pairs, about equal in length to the calyx in the flowering stage, lanceolate to broadly ovate, acute, five main nerves slightly prominent, the outer pairs anastomosing at the base; scarious, pubescent, only occasionally tinged with blue-purple. *Calyx* about 5 mm. long, pubescent to almost tomentose, margin ciliate, 15-nerved at the centre, though one or two pairs often anastomose near the base, slightly bilabiate,

3/2; median posterior tooth ovate-cuneate; lateral posterior pair ovate; anterior teeth ovate-lanceolate, reflexed in fruit. Corolla-tube less than double the calyx-length, exterior pubescent; lobes rather small. Nucules oblong or elliptic, 1.5 mm. long, pale to deep purplish brown, verruculose; areole small, obovate-rotund to oblate.

Distribution. Orient. SYRIA: (Wadi Zewerah Lowne). PALESTINE: (Ain Jidi Meyers & Dinsmore). ARABIA: Sinai (Dictaé ou Siédé Arab. Bové 55; Aucher-Eloy 1761; Schimper 231), Yemen (Botta), Arabia (Deflers 574).

N. Africa. EGYPT: Keneh and Kosser (Schweinfurth); Wadi Hof, Cairo (Volkens 175, Keller 133); Arabian and Mid-Egyptian deserts (Schweinfurth 183, 217).

NE. Tropical Africa. SUDAN: Darfur Province (Lynes 151, Rugman 9, Macintosh 40).

L. pubescens is a member of a group of closely allied species occurring in the Orient, Northern Africa, and the Atlantic Islands. Affinities with *L. multifida* Linn., *L. tenuisecta* Coss., *L. maroccana* Murb., *L. brevidens* (Humbert) Maire, *L. canariensis* Mill., and *L. stricta* Del. are evident. These species are distinguished by the leaves, by the conformation of the inflorescences, and by critical comparisons of indumenta, bracts, and calyces. They could with some justification be united together as subspecies of one 'common denominator', such as *L. pubescens* or *L. tenuisecta*, but for general convenience it seems preferable to retain them as species.

16. *L. STRICTA* Delile, Fl. Egypte, p. 238, t. 32 ('1812', but actually 1813).

Leaves lanceolate or ovate in outline, usually small, up to 2.5 cm. long, pinnate or \pm bipinnate; segments linear, acute to rounded; margins entire, revolute; segments not decurrent, the main rachis scarcely winged; the plants are frequently almost devoid of leaves. Indumentum of leaves hispid, of stems and peduncles typically glabrescent, sometimes densely pubescent. Peduncle and spike usually much branched, sometimes simple; spike lax, slender, elongating to as much as 20 cm. in fruit. Bracts paired, imbricate in the very young spike, usually biseriate, remote in older inflorescences, forming a flattened spike, lanceolate to broadly ovate, base truncate, apex acuminate, attaining $\frac{1}{2}$ calyx-length or less, scarious or tinged with pink, shortly pubescent or glabrescent; main nerves usually five. Calyx slender, tubular, 4.5–5 mm. long, becoming ovoid in fruiting stage; 15-nerved, 5-dentate, the teeth almost uniform, lanceolate-acute, about 1.5 mm. long, slightly reflexed in fruit. Corolla-tube double the calyx-length, about 9 mm. long, exterior pubescent; lobes small, deep blue-violet or sometimes pale. Nucule narrowly oblong, 1.5 mm. long, pale yellow-brown, minutely verruculose, with gelatinous envelope when soaked in water; areole small, \pm rectangular to oblate.

Distribution. Orient. PALESTINE. ARABIA PETRAEA (Schimper 141), Sinai (Bové 59, Ferieh Fischer 186), Midian Jeddah (Zohrab). EGYPT: (Delile), Cairo, Suez (Setouine 118), Central Egyptian Desert (Schweinfurth 256).

NE. Tropical Africa. RED SEA: Hanish Is. (*Slade* 16). ERITREA AND SUDAN: (approaching var. *subtropica*, *Lord*, *Schweinfurth* 246, 1076); Nubia (*Bent*), Darfur Prov. (*Lynes* 403 a), Red Sea Hills (*Aylmer* 229, 253; *Maffey* 3, 42 b). CENTRAL SAHARA: Ahaggar (*Maire* 938, 943; *Chudeau*), Arak (*Maire* 930), Abelessa (*Chipp* 44). MAURITANIA (*Chudeau*, approaching var. *subtropica*).

Atlantic Islands. CAPE VERDE IS. (*Milne*; *Welwitsch* 5523).

Synonyms.—*L. coronopifolia* Poir. *Encycl. meth. Suppl.* III, p. 308 (1813).

This name has been generally used for the species, but, owing to the priority of publication of the name *L. stricta* Delile, the latter is correct. Both names were based on material collected by Delile in Egypt, Val de l'Egaremont, Suez Desert.

L. striata Boiss. (*Fl. Or.* iv, p. 542; 1879) is an error for *L. stricta* Del.

Varieties.

β . SUBTROPICA *Chaytor*, comb. nov. [*L. subtropica* Gand. in *Bull. Soc. Bot. Fr.* LXV, p. 66 (1918)].

This variety differs from the type chiefly in its more dense *indumentum*, but also in leaf and inflorescence characters. The *stem* is pilose-scabrous, the *leaves* hirsute with stiff hairs, the *calyx* shortly grey pubescent; the leaf-segments oblong, obtuse, margins only slightly revolute; the *spike* is lax, \pm 4-seriate, the *bracts* arranged in \pm opposite pairs, bracts rather larger than those of the type; posterior calyx-tooth broadly lanceolate, the others uniformly lanceolate.

Distribution. Tropical Atlantic Is. CAPE VERDE IS.: (S. Antão *Cardoso*, Santiago ad la Praya *Thiébaut* 225, quoted by Gandoger. There are also specimens at Kew, *Cardoso* 31, *Welwitsch* 5.523, Sta. Nicolão *Lowe*, *Bolle*, St. Vincent *Milne*, and *Vogel* 24 and 48 from St. Antonio and St. Vincent respectively; this material is heterogeneous, some approaching the type fairly closely). North Tropical Africa. SUDAN, Suakin (*Lord*, *Schweinfurth* 246). MAURITANIA (*Chudeau*). The variety probably occurs over the whole distribution of the species.

γ . HUMBERTII *Chaytor*, comb. nov. [*L. Humbertii* Maire & Wilczek in *Bull. Soc. Hist. Nat. Afr. Nord*, xxv, p. 314 (1934)].

This variety was described as a species by Maire and Wilczek (loc. cit.), but it differs from the type only in the retrorse, adpressed, shortly pubescent lower *stem-indumentum*, in the \pm imbricate to biseriate *spike*, in the rather broader *bracts*, larger *calyx* (6 mm. long), and in the rather broader *nucule*. The corolla is pale blue-violet. The plant is evidently the N. African facies of *L. stricta* Delile.

Distribution. North Africa. MOROCCO: (Taoumart, 950 m., *Maire* 1700; Akka, Tatta, *Maire*; Oued Drâa 575, and Azlag 527, *Malençon*).

17. L. SOMALIENSIS Chaytor, sp. nov.

Suffrutex, caule perenne circiter 5 cm. alto et 0·5–2 cm. diam. tortuoso lignoso, ramis annuis virgatis ascendentibus 10–40 cm. longis. *Indumentum* tomentoso-lanuginosum, pilis albis tenuiter ramosis et glandulis fere sessilibus. *Folia* pinnata vel pinnato-dentata, segmentis latis ovatis vel oblongo-ovatis integris apice rotundatis basi plus-minusve truncatis. *Spicae* haud ramosae, cylindricae. *Bracteae* lanceolatae, acuminatae, 5–6·5 mm. longae, calyci subaequales. *Calyx* sub-bilabiatus, dentibus 2 abaxialibus ovato-lanceolatis, 3 adaxialibus ovatis inter se fere aequalibus. *Corollae tubus* calyci duplo longior, lobis bilabiatis 2 adaxialibus circiter 4 mm. longis erectis.

The habit of this species is peculiar ; the young leafy shoots, with the inflorescences, appear to be replaced annually, always arising from the apex of the short main stem or from the extreme base of previous shoots, which are broken off a short distance above their attachment to the main axis. This lack of older shoots may be due to grazing by animals, but it is a constant feature of all the specimens at Kew (11 in number). The indumentum is most dense on the youngest stems and leaves, becoming more sparse as these age ; small globular sessile glands are present on the lower surface of the leaf, sometimes also on bracts and calyces. The leaves are ovate in outline, up to 3·5 cm. long including a petiole 0·3–1 cm. ; the median rachis is broad, winged ; the margins of the segments are slightly revolute ; nerves prominent on the lower surface. Peduncle unbranched, up to 12 cm. long. The spike is terminal on primary and lateral branches, oblong, up to 4 cm. long. The bracts are arranged in exactly opposite pairs, often \pm in whorls of 4, rather sparsely grey tomentose. The calyx is cylindrical, 15-nerved, sparsely tomentose, slightly inflated in the fruiting condition, the anterior teeth reflexed, the margins of the teeth ciliate with longer hairs. Exterior of corolla-tube tomentose, probably pale purple or blue, but I have seen no living specimens. Nucule oblong, 1·75 mm. long, deep red-brown when mature, lacking a gelatinous envelope when soaked in water.

Distribution. NE. Tropical Africa. BRITISH SOMALILAND : collected by the Drake-Brockman expedition in Golis Range, Fodyer (Fodiyer), nos. 505, 506, 519 (type), 520, 521, rec. Kew, 1908 ; nos. 547, 548, 549, 555, coll. Dec. 1909, 5750 ft. ; nos. 1158, 1159 coll. March 1914, rec. Kew, 1915.

The slender ascending stems and the general shape of the leaves suggest a relationship with certain S. Arabian and Socotran species (*L. subnuda* Benth., *L. Nimmoi* Benth., *L. setifera* Anders., *L. macra* Baker) of section *Subnuda*, but the opposite paired arrangement of the bracts of *L. somaliensis* excludes it from that section.

18. L. PINNATA Linn. f. De Lav. p. 11 (1780).

Leaves obovate or elliptic in general outline, up to 8·5 cm. long including petiole up to 3 cm., the base slightly dilated ; pinnate, sometimes bipinnately-lobed, margins entire somewhat revolute, segments oblanceolate to oblong-linear, obtuse or rounded, the terminal segment often very broad at the apex, \pm bifid

or trifid. *Indumentum* of whole plant incanous, a dense grey felt of very short branching hairs. Base of *spike* often much branched, spikes compact, cylindrical, up to 9 cm. long. *Bracts* in alternating pairs, \pm imbricate, lanceolate, grey or tinged with blue-purple, nerves 5, rather indistinct; 2–3 mm. longer than the calyx in the flowering stage and concealing the calyx almost entirely. *Calyx* 4–5 mm. long, 15-nerved, grey canescent or tinged with blue-purple, bilabiate, anterior teeth lanceolate, posterior teeth ovate to deltoid, teeth spreading in fruiting stage. *Corolla*-tube nearly double calyx-length, about 8 mm. long. *Nucules* about 1.5 mm. long, oblong, typically purplish brown; areole obovate, about $\frac{1}{2}$ length of nucule.

Distribution. Atlantic Islands. MADEIRA: (Gay 153; Lowe 53; Mandon 192); CANARY IS.: Lanzarote (Bourgeau 903; Lowe 74). The var. *Buchii* Benth. (see below) occurs in the Canary Is., Teneriffe, and Lanzarote.

Synonyms.—*L. pinnata* Jacq. Misc. Austr. II, p. 318 (1781), et Ic. Rar. I, II, t. 106 (1781–86). *L. pinnatifida* Salisb. Prodr. p. 79 (1796). *Stoechas pinnata* Reichb. f. in Oestr. Bot. Woehenbl. VII, p. 161 (1857).

Varieties.

β . *BUCHII* Benth. in DC. Prodr. XII, p. 146 (1848).

This variety is distinguished from the type by its shorter ovate *bracts*, 1–3 mm. shorter than the calyx, and by the paler *nucules* with smaller areoles. The leaf-segments tend to be narrower than those of the type. The variety was originally described as a species, *L. Buchii*, by Webb and Berthelot (Phyt. Canar. III, p. 58; 1836); the petioles were described as scarcely dilated at the base, and the spike as more lax than in *L. pinnata*, though these points do not seem constant.

Distribution. Atlantic Islands. CANARY IS.: Teneriffe (Webb, 1848; Berthelot, 1850; Bourgeau 69, 1475); Lanzarote (Kuntze 1.1888, Risco de Famara).

Gingins de Lassaraz (Hist. Nat. Lav. p. 159; 1826) divided the species into three varieties, based on the shape of leaves and leaf-segments; these seem to fluctuate rather irregularly and Gingins' varieties have not been maintained by later authors.

L. formosa Dietr. (Lexic. Nachtr. p. 4; 1818) is quoted by Gingins (op. cit. p. 162) as a doubtful synonym for *L. abrotanoides* Lam. According to Bentham (Lab. I, p. 150) this species is a German cultivated form of *L. pinnata* which he calls var. *pubescens*, less densely incanous and with more lax spikes. I can find no mention of *L. formosa* in Dietrich's 'Lexicon der Gartnerei und Botanik'.

L. formosa Link (Enum. hort. Berol. II, p. 103; 1822) is certainly a form of *L. pinnata*; Link says 'folia pinnata pubescentia, spica composita laxa. Differt a *L. pinnata* uti *L. abrotanoides* a *L. multifida*'. Gingins quotes *L. formosa* Link, under his var. β ; Bentham (Lab. Gen et Sp. I, p. 150) considered that *L. formosa* of Link and of Dietrich were identical, quoting both under his var. *pubescens*. Later (in DC. Prodr. XII, p. 146) he renamed this variety *formosa*, but provided no description.

19. *L. foliosa* Christ in Engl. Bot. Jahrb. IX, p. 130 (1888).

Leaves petiolate, up to 8 cm. long and 4 cm. broad, ovate acute in outline, regularly pinnate from base to apex ; rachis broadly winged (3–4 mm.) ; lower segments 3- or 2-lobed, acute lanceolate elongate, upper segments entire, \pm pectinate, terminal segment cuneate, \pm 2- or 3-lobed. *Stems* tall, foliose, with 5–6 pairs of leaves or more, internodes 6 cm. *Indumentum* of slender hairs, short sparse pubescent ; plant green. *Peduncles* very long, *spikes* branching. *Bracts* ovate-oblong, rather longer than the calyx ; *calyx-teeth* ovate, acute, ciliate.

Distribution. Atlantic Is. CANARY Is. : Grand Canary (Valle Tirajana, Bourgeau It. II, 1471, de Noë).

Christ notes that *L. foliosa* differs from all the species of the Atlantic Islands [he does not mention *L. rotundifolia*] in the long internodes and foliose stems ; it resembles *L. pinnata* Linn. f. in the general outline of the leaves, but differs in the pubescent hirsute indumentum. *L. abrotanoides* is distinguished from *L. foliosa* by the crowded leaves at the bases of the stems, the general outline and much narrower linear obtuse remote segments of the leaves, and the broadly ovate bracts of the former. *L. foliosa* differs from *L. Minutolii* in the more sparse indumentum, not grey tomentose, and in the size and shape of the leaves.

L. foliosa is evidently intermediate in leaf-shape, general indumentum, and bract characters between *L. pinnata* and *L. Minutolii*. O. Kuntze (Revis. Gen. Pl. p. 522 ; 1891) suggests that *L. foliosa* is a synonym for *L. Minutolii*, and that the specimen quoted by Christ—Bourgeau no. 1471—is a misprint for no. 1477 which is *L. Minutolii*, with identical data on the labels. I have not been able to examine the type-specimen of *L. foliosa*, but the original description clearly indicates the important characters.

20. *L. MINUTOLII* Bolle in Bonpl. VIII, p. 279 (1860).

Leaves lanceolate or ovate in outline, up to 4·5 cm. long, including petiole up to 1·5 cm., up to 2 cm. broad, very regularly closely pectinate-pinnate ; segments entire, linear, margins slightly revolute ; apex rounded or acute. *Stems* erect, branching, with numerous leaves on the young shoots. *Indumentum* of leaves and young stems grey floccose-tomentose ; older stems dark, sparsely tomentose ; peduncles tomentose-hirsute ; hairs slender, branching. *Peduncle* and *spike* simple or branched ; spike compact, cylindrical, 2·5–8 cm. long. *Bracts* paired, alternating, broadly ovate, pubescent, tinged with deep blue-purple, slightly longer than the calyx in flowering condition ; nerves 5, prominent, dark purple. *Calyx* 4 mm. long, bilabiate, teeth spreading at fruiting stage, 15-nerved, tomentose-pubescent, the margin shortly grey ciliate. *Corolla-tube* rather more than double the calyx-length. *Nucule* smooth, brown, 1·25 mm. long, elliptic-oblong ; areole broadly obovate, about $\frac{1}{3}$ nucule length.

Distribution. Atlantic Islands. CANARY Is.: Grand Canary (Valle de Tiraxana, Bourgeau 1477; Lowe; Fatalga, Murray in Herb. Barbey-Boiss.).

Synonym.—*L. Buchii* Webb var. *Tirajana* Pitard & Proust, Fl. Iles Canar. p. 299 (1908). These authors suggest that this variety is equivalent to *L. Minutolii* Bolle. Their description agrees with this, though they do not mention the very characteristic pectinate-pinnate leaf.

L. Minutolii appears to be related to *L. abrotanoides*, *L. foliosa*, and *L. pinnata* var. *Buchii*. The differences lie chiefly in the leaves and indumentum.

21. *L. ROTUNDIFOLIA* Benth. Lab. Gen. et Sp. 1, p. 150 (1833).

Leaves up to 6 cm. long including petiole up to 1·5 cm., rotund, broadly ovate or ovate-triangular, margins irregularly dentate, apex rounded, base rounded or truncate. Indumentum of stem, peduncle, and spike short dense pubescent, longer hairs at margins of calyx; of leaves, short, sparse pubescent. Peduncle and base of spike branching; spike cylindrical, compact, up to 7 cm. long. Bracts arranged in opposite alternating pairs; lanceolate or ovate-acute, 1–2 mm. shorter than the calyx at the flowering stage; tips and nerves sometimes purplish. Calyx 5 mm. long, 15-nerved, scarcely bilabiate; four anterior teeth uniform, ovate-lanceolate; median posterior tooth slightly broader; teeth and nerves often purplish. Corolla-tube more than double the calyx-length, about 12 mm. long; exterior of the tube and the lobes pubescent. Nucule 1·75 mm. long, narrowly oblong, minutely granular, pale or deep purple-brown; areole obovate-rotund.

Distribution. Temperate and Tropical Atlantic Islands. MADEIRA : (Lowe); CAPE VERDE Is. (St. Nicholas, Forbes, Cardoso, Bolle).

Synonyms.—*L. apiifolia* C. Smith in Tuckey, Congo, p. 250 (1818). *Stoechas rotundifolia* Reichb. f. in Oestr. Bot. Wochensbl. VII, p. 161 (1857).

In Tuckey's 'Congo', at p. 243, Smith mentions that in the Cape Verde Is. he discovered 'a beautiful new Lavendula and several others met with in the Canaries'. Later, on p. 250, in a list of indigenous plants of the Cape Verde Is., he gives '*Lavendula apiifolia* sp. nov. ms.' Apparently he never published a description, but the plant was probably *L. rotundifolia* Benth.

Varieties.

β. *SUBPINNATIFIDA* Lowe ms., var. nov.

This variety is distinguished by leaf, indumentum, and inflorescence characters. The leaf is ovate or lanceolate, the margins irregularly laciniate-dentate or subpinnate, apex acute, base cuneate; indumentum of leaf, stem, and peduncle sparsely hirsute or glabrous; inflorescence usually much branched, the spikes long, up to 10 cm.; bracts $\frac{1}{2}$ calyx-length in flowering stage; corolla-tube nearly double the calyx-length, 9–10 mm. long.

This variety occurs together with the type in the Cape Verde Is., and was collected by Lowe (13. iii. 1864); Vogel (5, 77), Moseley (Challenger Expedition no. 10), and others in Fogo Is., St. Vincent, and St. Antonio. Wawra (Bot.

Ergebn. Reise Maximilian, p. 95, t. 69 (1866)) gives a description and drawing of *L. rotundifolia* Benth. exactly corresponding with var. *subpinnatifida*. Schmidt (Beitr. Fl. Cap Verd Ins. p. 218; 1852) in a note under *L. rotundifolia* mentions plants which would belong to this variety.

γ. CRENATA *Lowe* ms., var. nov.

This plant differs from the type in its ovate-rotund leaves with very regularly crenate (not dentate or lacinate-dentate) margins, the apex rounded, the base subcuneate. The *indumentum* is also distinctive, the stems and petioles being hirsute over a short pubescence, and the peduncles pubescent. The type of this variety was collected by *Lowe* (12. ii. 1864), in St. Nicholas, Cape Verde Is.

22. *L. ATRIPLICIFOLIA* Benth. in DC. Prodr. XII, p. 146 (1848).

Leaves narrowly elliptic, up to 2·5 cm. long, entire; apex acute; base attenuated into a short petiole; midrib prominent on the lower surface. Internodes of the upper parts of the stem long: pairs of leaves are found on the inflorescence axis. *Indumentum* of leaves, stems, and peduncles incanous, densely shortly white-tomentose. *Peduncles* and bases of *spikes* ± ternately branched; peduncles short, up to 6 cm., but usually less; spike compact, imbricate-quadrata, up to 4 cm. long. *Bracts* broadly obovate to rotund, apiculate, scarious, glabrous or sparsely glandular, margins ciliate, three main nerves, the outer pair branched: bracts equal in length to the calyx in flowering stage. *Calyx* 4 mm. long, 5-dentate, scarcely bilabiate, the teeth almost uniform, 15-nerved (13 quite at the base), tomentose. *Corolla*-tube less than double the calyx-length, about 6·5 mm. long, externally pubescent; lobes about 2·5 mm. long, narrow, lanceolate, almost uniform, the posterior pair slightly broader. *Nucule* 1·75 mm., narrowly elliptic-oblong; areole $\frac{1}{4}$ length of nucule.

Distribution. Orient. ARABIA: Yemen (NE. Dj. Nugum, 2400 m., *Deflers*, in Herb. Paris).

N. Africa. UPPER EGYPT (*Frigari*, *Parlatore*).

Synonym.—*L. canescens* *Deflers*, Voy. Yemen, p. 186 (1889), who says that his plant is certainly very near *L. atriplicifolia* Benth. and only hesitates to identify the two because the bract arrangement differs; in Benthams's plant the bracts are opposite, paired, while *Deflers* described those of his type as alternate. I have examined both type-specimens, and they are evidently identical; the bract arrangement may fluctuate very slightly, but the two plants agree very closely.

HYBRIDS OF THE SECTION PTEROSTOECHAS.

L. CANARIENSIS Mill. (*L. abrotanoides* Linn.) \times *L. PINNATA* Linn. fil.

This hybrid was recorded by Christ (in Engl. Bot. Jahrb. ix, p. 130; 1888), who diagnosed a plant sent to him by Bolle under the name *L. Buchii* from

Taganana, Teneriffe, as a hybrid between *L. pinnata* var. *Buchii* and *L. canariensis*, giving the following description :—‘Habitus *L. pinnatae*, sed praeter tomentum brevissimum albicans plus minus evanidum pilis numerosis pubescens, pedunculo infra spicam manifeste villoso, foliorum lobis multo angustioribus, inferioribus quoque latus 3 aut 2 lobis lobulis patentibus.’ A specimen collected by Murray in Val Bufadero, Teneriffe, also agrees with this description.

Pitard and Proust (Fl. Iles Canar. p. 299 ; 1908) record a hybrid of *L. canariensis* with *L. pinnata*, quoting specimens from Teneriffe, Taganana (coll. Bornmüller), and Barranco de Bufadero, growing amongst the parents, but give no description.

L. MAROCCANA Murb., ♀ × *L. MULTIFIDA* Linn., ♂.

Murbeck (in Bull. Soc. Hist. Nat. Afr. Nord, p. 331 ; 1934) described the hybrid, which appeared in the Lund Botanic Garden amongst seedlings from *L. maroccana*, as follows :—‘*Caulis* basin versus pilis ± elongatis parce conspersus. *Bracteae* calyce deflorato subdupo breviores, explanatae suborbiculares, breviter cuspidatae. *Calyx* tubulosus, ob nuculas abortivas etiam post anthesim basi non dilatatus. *Calycis labium inferiorius* [superius] leviter tridentatum ; *dentes labii inferioris* etiam post anthesin erecti. *Planta* calyce deflorato excepto inter species dictas omnino intermedia. *Grana pollinis* fere omnia (95–98 %) tabescentia ; nuculae omnes abortivae.’

SECTION IV. CHAETOSTACHYS Benth. Lab. I, p. 151 (1833).

Genus *Chaetostachys* Benth. in Wall. Pl. As. Rar. II, p. 19 (1831).

Herbaceous plants with thick green stems and numerous leaves. Peduncles and spikes often much branched. Bracts alternately or ± spirally arranged, single flower in axis of each. Calyx 15-nerved, slightly bilabiate. Areole attaining $\frac{2}{3}$ the length of nucule, or more. India.

The first species of this section to be described was *L. bipinnata* Kuntze as *L. multifida* by Burman (Fl. Ind. p. 126, t. 38 ; 1768). It was later described as *Bystropogon bipinnatus* by Roth (Nov. Pl. Spec. p. 255 ; 1821), and as a distinct genus *Chaetostachys multifida* by Bentham (in Wall. Pl. As. Rar. II, p. 19 ; 1831) ; but Bentham reduced it to *Lavandula* in his ‘Labiatae’ (I, p. 151 ; 1833), placing it in a new section, *Chaetostachys*. Later (in DC. Prodr. XII, p. 147 ; 1848) he included *L. subnuda* and *L. Nimmoi* in his section *Chaetostachys* ; but these, with *L. macra* and *L. setifera*, are quite distinct from the Indian species *L. bipinnata* (*L. Burmanni* of Bentham) and *L. Gibsoni*, and are here separated from the section *Chaetostachys* by transfer to the section *Subnuda*. These two sections differ in habit, in the size and abundance of the leaves, in the branching of the spikes, and in the size and shape of the areole of the nucule ; they occur in widely separated areas, with, so far as is known, no intermediate stations. Together they differ from the other three sections

of *Lavandula* in the alternate or \pm spiral arrangement of the bracts. The 15-nerved calyx was supposed by Bentham to be diagnostic of his section *Chaetostachys*, as both Gingins de Lassaraz (Hist. Nat. Lav. p. 104 et seq.; 1826) and Bentham give 13 as the number of nerves in the calyx of the other three sections. I have examined numerous specimens of these sections, and while the calyces of *Stoechas* and *Spica* are undoubtedly 13- (or 8-) nerved, those of all species of *Pterostoechas* are 15-nerved. The leaf-shape is not sufficiently constant to be used in sectional diagnosis. O. Kuntze (Rev. Gen. Pl. p. 521; 1891) makes only two species in section *Chaetostachys* Benth. (*Chaetostachys* emend. and *Subnuda*), *L. Gibsoni* Grah. and *L. bipinnata* Kuntze. He includes all the other species (except *L. macra* Baker, which was not described till later) in *L. bipinnata* as subspecies. I do not agree with this arrangement, on the grounds that there are fundamental differences between the Indian and the Arabian and Socotran species.

KEY TO THE SPECIES OF SECTION CHAETOSTACHYS.

Bracts conceal calyx	23. <i>L. Gibsoni</i> .
Bracts cover only basal part of calyx	24. <i>L. bipinnata</i> .

DISCUSSION OF THE SECTION CHAETOSTACHYS.

23. *L. Gibsoni* Grah. Cat. Pl. Bombay, p. 149 (1839).

Plant herbaceous, up to 1 metre in height. Stem rectangular, slightly contracted at the nodes; internodes long (often 10 cm. or more). Indumentum of the whole plant short, dense, pilose. Leaves \pm petiolate, pinnate-dentate with broad central lamina, pinnate or \pm bipinnate, the segments narrowly oblong, oblong or elliptic, obtuse; up to 13 cm. long. Inflorescence branched (main axis and at base of spikes); spikes dense, imbricate, narrowly oblong, up to 5.5 cm. long. Bracts herbaceous, green, broadly lanceolate, acute, densely hirsute, arranged \pm alternately in flowering condition, though probably displaced by the growth of the inflorescence axis from an early opposite paired arrangement; about 7.5 mm. long, equal to or slightly longer than the calyx and almost entirely covering it from view. Calyx tubular, 7 mm. long, 15-nerved, bilabiate 3/2, the teeth of equal breadth, the two anterior longer. Corolla-tube \pm 1½ calyx-length; lobes rather small. Nucules dark brown, 2 mm. long, white arcole oblong-lanceolate covering about $\frac{3}{4}$ of length of the outer surface.

Distribution. INDIA: Madras and Bombay Presidencies Nilgherries (Perrottet), Concan (Hooker fil. & Thomson), Bombay (Herb. N. A. Dalziel), Satara (ex Herb. Wight).

Synonyms.—*L. Perrottetii* Benth. in DC. Prodr. xii. p. 147 (1848). *L. Lawii* Wight. Ic. t. 1439 (1849).

Graham gives as description only 'Herbaceous, leaves lyrate'. He adds that the type requires examination, and the note 'probably this is only a young

plant of the next species [*L. Burmanni*] which begins to flower within ten days or a fortnight after it has sprung up ; though it afterwards grows in a good soil to a height of 2 or 3 feet (Mr. Law) '.

24. *L. BIPINNATA* Kuntze, Revis. Gen. Pl. p. 521 (1891).

Plant herbaceous, 0·15–1 m. in height. *Stem* rectangular, somewhat contracted at the nodes. Internodes up to 12 cm., but often about 5 cm. *Indumentum* of whole plant shortly pubescent, dense on the stems and inflorescence, more sparse on the leaves. *Leaves* 2–12 cm. long, sessile or shortly petiolate, pinnate or \pm bipinnate ; segments up to 5 cm. long, linear to oblong in the mature plant, broadly oblong or lyrate when the plant is young ; the central rachis \pm broadly winged ; margins entire ; apex acute, rounded, or obtuse. *Inflorescence* \pm branching, both from the main axis and at base of spike, eventually becoming almost umbellate in some cases ; the spike densely imbricate, narrowly oblong, usually about 4 cm. long, up to 7·5 cm. *Bracts* membranous, pubescent, ovate, acute to long-acuminate or setose, alternate though probably derived from an opposite paired arrangement in the very young stages ; 2–10·5 mm. long, concealing only the base of the calyx. *Calyx* densely pubescent, cylindrical, becoming ovoid in fruiting stage ; 15-nerved, the nerves often dark bluish at teeth, 5-dentate, bilabiate ; anterior teeth lanceolate ; posterior ovate ; calyx 4–6 mm. long. *Corolla-tube* nearly double the calyx-length, externally pubescent ; bilabiate, lobes rather small. *Nucules* brown, 2·5 mm. long, white areole lanceolate, forming a groove along practically the whole length of the outer surface.

Distribution. Central and S. INDIA, Bombay to Bengal and southwards. Variation occurs in the size of the plant, in leaf-size and shape, in degree of branching of the inflorescence, in the shape and actual length of the bract, and in its length relative to the calyx. The habit and size of the plant and leaves and the degree of branching of the inflorescence seem to be determined largely by the ecological conditions as governed by the altitude ; plants from the low-lying regions, e.g. of Bombay and Madras, tend to be taller and with larger leaves than those from the higher regions of Indore and Hyderabad.

O. Kuntze (Revis. Gen. Pl. p. 521 ; 1891) uses the variation in bract-characters to divide the species into three varieties, though he takes little account of the differences in vegetative organs :—

Varieties.

$\alpha.$ *BURMANNIANA* Kuntze, Revis. Gen. Pl. p. 521 (1891).

Bracts not aristate, shorter than the calyx, broadly ovate acute, or obovate apiculate, about 1·5 mm. long, approximately $\frac{1}{2}$ calyx-length.

Distribution. INDIA : Concan (Konkan) (Herb. Hooker fil. & Thomson, coll. Stocks, Law).

β . *Rothiana* Kuntze (loc. cit.) (*L. Burmanni* Benth.).

Bracts ovate or lanceolate, apex long aristate (setose) up to 4 mm. longer than the calyx.

Distribution. INDIA. Indore (*Jacquemont* 145, 456), Hyderabad, Aurungabad, Dowlatabad, Ellora (*Jacquemont* 254), Bombay, Concan (Herb. Hooker fil. & Thomson, coll. *Stocks, Law*), Salsette (Herb. *Hook.*), Bombay (Herb. *Dalzell*), Rajputana (Mt. Abu, *Duthie* 6801, *Gamble* 21008), Madras (Herb. *Wight* 2124, 2524, 2117 ; *Wallich*), Canara and Mysore (*Law*), Bellary (*Lushington*).

γ . *INTERMEDIA* Kuntze (loc. cit.).

Bracts lanceolate, shortly acuminate, shorter than the calyx by at least 1 mm.

Distribution. INDIA : Bombay, Concan (Herb. Hooker fil. & Thomson, coll. *Stocks, Law*), Central Provinces, Sonawani Range (*Haines* 3472), Bengal, Chagpul (coll. *Johnston*, Herb. *Gamble*), Chota Nagpur, Jaigu (Palamau, 2000 ft., *Gamble* 8760).

Synonyms.—*L. multifida* Burm. Fl. Ind. p. 126, t. 38. i. (1768). The description is inadequate and might refer to either Indian species, though taken together with the figure it evidently refers to *L. bipinnata*. The figure has been generally considered to represent *L. coronopifolia* (see Benth. Lab. I, p. 151), but almost certainly represents *L. bipinnata* var. α . *Burmanniana*. *Bystropogon bipinnatus* Roth, Nov. Pl. Spec. p. 255 (1821). *Chaetostachys multifida* Benth. in Wall. Pl. As. Rar. II, p. 19 (1831). Bentham at first described the plant as a separate genus, but afterwards (Lab. I, p. 151 ; 1833) included it in *Lavandula*. *L. Burmanni* Benth. Lab. Gen. et Sp. I, p. 151 (1833).

From the description and quoted specimens, *L. Burmanni* Benth. corresponds to the var. *Rothiana*. Kuntze says that 'Bentham either did not know or overlooked the var α , or else thought Burman had made a mistake in his drawing of *L. multifida* Burm. (nec Linn.) Fl. Ind. t. 38, i'. But Burman's drawing is correct and corresponds with the var. α known to me. This is seen in the Kew Herbarium in an example from Concan, collected by *Stocks* (*Law*) with β . *Rothiana* and γ . *intermedia*.

SECTION V. SUBNUDA Chaytor, sect. nov.

Frutices parvi a basi ramosi, ramis siccis lignosis, at junioribus plus-minusve herbaceis, foliis saepissime paucis. Pedunculi saepissime ramosi, spicis simplicibus. Bracteae alternatae vel plus-minusve spirales, floribus in bractearum axillis solitariis. Calyx 15-nervius, leviter bilabiatus. Areola quam nucula $\frac{1}{2}$ - $\frac{2}{3}$ brevior. S. Arabia et Socotra.

The points of difference between species of this section and those of section *Chaetostachys* and the other sections of *Lavandula* are discussed above under section *Chaetostachys*.

KEY TO THE SPECIES OF SECTION SUBNUDA.

Bracts lanceolate, sometimes shortly acuminate, not exceeding calyx in length.

Stems shortly pubescent or glabrescent; posterior calyx-teeth of equal breadth.

Stems branching chiefly at the base; leaves present in adult plants. 25. *L. subnuda*.

Stems branched throughout their length; leaves almost entirely absent in adult plants 26. *L. macra*.

Stems \pm densely villous, especially at base of young shoots; median posterior calyx-tooth broader than the others 27. *L. Nimmoi*.

Bract narrowly lanceolate, long setose acuminate, exceeding calyx in length (up to 4 mm. longer) 28. *L. setifera*.

SPECIES OF THE SECTION SUBNUDA.

25. *L. SUBNUDA* Benth. in DC. Prodr. XII, p. 148 (1848).

Bushy plants, much branched and leafy at the base with long slender erect leafless flowering shoots, up to 50 cm. high. *Stems* erect, square, 4-ribbed; *indumentum* of fine hairs, densely pubescent to glabrescent. *Leaves* pubescent, lyrate to obovate-dentate, the lower lobes deeply incised oblong, base cuneate, up to 3 cm. long including petiole about $\frac{1}{3}$ of the length of the lamina; leaves few, confined to the basal regions and to a few herbaceous shoots. *Peduncle* long, slender, branching. *Spike* unbranched, narrowly oblong, rather lax imbricate, up to 8.5 cm. long. *Bracts* spirally arranged, lanceolate, acuminate, slightly shorter than the calyx at the flowering stage, though the calyx elongates later, shortly pubescent. *Calyx* oblong, about 5.5 mm. long, scarcely bilabiate 5-dentate, the teeth lanceolate, the three posterior slightly shorter; 15-nerved; shortly grey pubescent; mouth closed by grey hairs projecting inwards from interior of calyx-teeth. *Corolla-tube* 10-11 mm. long, exterior pubescent, bilabiate, posterior lobes about 2.5 mm. long. *Nucule* oblong, about 1.5 mm. long, deep purple-brown; areole about $\frac{1}{4}$ nucule length, triangular.

Distribution. Orient. SE. ARABIA: Oman, in the kingdom of Muscat (Aucher 5220), Semail (*Pilgrim*).

L. subnuda is diagnosed by the leaves, which are unique in the genus. Habit and inflorescence-characters are also typical.

26. *L. MACRA* Baker in Kew Bull. 1894, p. 339.

A dense bushy plant, 30-60 cm. high, with slender stems almost destitute of leaves. *Stems* \pm erect, much branched throughout their length, slender, quadrate, with 4 main and 4-12 subsidiary ribs, glabrescent to very shortly grey pubescent. *Leaves* entirely absent from most specimens, only one small leafy shoot present on material at Kew; the leaves here are lyrate, the apical segment elliptic, the one pair of lateral segments \pm triangular, shortly pubescent, about 1 cm. long, including petiole about 2 mm. long. *Spikes* cylindrical, rather lax to densely imbricate, up to 6 cm. long, unbranched. *Peduncles*

often short (2–5 cm.), branching, very slender. *Bracts* ovate or lanceolate, acuminate, 2–4 mm. long, much shorter than the calyx, shortly pubescent, spiral or alternate. *Calyx* slender, tubular, 4·5–5·5 mm. long, 15-nerved, \pm bilabiate, 5-toothed, shortly pubescent with numerous short grey hairs on the interior of the teeth. *Corolla-tube* 8–10 mm. long, exterior pubescent; lobes small (1–2 mm. long), slightly bilabiate; corollas blue. *Nucule* pale brown or greenish brown, about 1·3 mm. long, elliptic-oblong; areole about $\frac{1}{2}$ as long as the nucule, oblate.

Distribution. Orient. S. ARABIA: Hadramaut (Bakrain near Mokalla, 200 ft., no. 60, and Khailah, 3000 feet, no. 135, Th. Bent coll. Lunt), Oman, Muscat (Bornmüller no. 564).

L. macra Baker is nearly allied to *L. subnuda* Benth., from which it differs chiefly in habit; the stems are branched throughout their length, not chiefly at the base as in *L. subnuda*, and the leaves are practically absent; also to some extent it differs in the very short pubescent indumentum, and in the shorter bracts, smaller corolla-lobes, and pale colour of the nucule.

27. *L. NIMMOI* Benth. in DC. Prodr. XII, p. 148 (1848).

Plants herbaceous with numerous leaves, or small scrubby bushes with only few small leaves, up to 45 cm. high. Habit probably determined by ecological conditions. Stems branching chiefly at the base, erect or ascending, slender, \pm squarely 4-ribbed, \pm densely villous below, sparsely villous or hirsute to glabrous above. Leaves pinnate-dentate or pinnate, segments broad, oblong to obovate, obtuse, entire or dentate, petioles fairly long, $\frac{1}{2}$ to $\frac{1}{4}$ length of the lamina. In young plants and probably those growing in moist places the leaves are large, lanceolate in outline, up to 5·5 cm. long and 2·5 cm. broad; in the bushy xerophytic types the leaves are oblong-lanceolate, very small, 1–2 cm. long and 0·5 cm. broad, pinnate-dentate, the margins much revolute. Spike unbranched, slender, rather lax imbricate, often short (about 2 cm.), but reaching 6 cm. Peduncles slender, sometimes branched. Bracts lanceolate or ovate, acuminate, 1–3 mm. shorter than calyx, \pm tomentose-villous to hirsute; alternate. Calyx 5–5·5 mm. long, oblong, grey-hirsute, bilabiate, 5-dentate, the posterior tooth broader than the others; nerves 15. Corolla-tube 6–7 mm. long, exterior pubescent, bilabiate. Nucule oblong, about 1·3 mm. long, deep red-brown; areole about $\frac{1}{2}$ as long as the nucule, rotund.

Distribution. NE. Tropical Africa. SOCOTRA (*Nimmo*, Balfour 486, 507, 689; Tamrida no. 361, Scheheli-Kegel, 1200 m., no. 657, Schweinfurth).

Variation occurs in the habit, in leaf-size and abundance, and in stem indumentum.

L. Nimmoi is diagnosed by the villous indumentum of the lower parts of the stem and by the \pm tomentose inflorescence. Leaves, habit, and calyx-teeth are also typical.

28. *L. SETIFERA* Anders. in Journ. Linn. Soc. Lond. v, suppl. 1, p. 29 (1860).

Lax bushy plants, erect or ascending, up to 50 cm. high including flowering spikes, internodes long and leaves few and rather small, or almost entirely absent. *Stems* often \pm terete 8-ribbed, occurring together with square 4-ribbed stems on most plants; branching occurs chiefly at lower nodes; branches long, slender, rather wiry, glabrescent to pubescent. *Leaves* 1-2.5 cm. long including a short petiole, oblong to ovate, pinnate-dentate to pinnate, the segments short up to 1 cm. long, entire or dentate, oblong or \pm ovate, margins plane or slightly revolute; indumentum shortly hispid, especially on nerves of lower surface, to shortly and densely pubescent; leaves often almost absent from older plants. *Spikes* unbranched, oblong, usually 3-4 cm. long, up to 6 cm., densely imbricate. *Peduncles* long, slender, unbranched. *Bracts* lanceolate or ovate, the apex setaceous-acuminate, forming an apical tuft in young inflorescences, exceeding the calyx in the flowering state by 1-4 mm., spirally arranged. *Calyx* 5 mm. long, slender, tubular, pubescent, 15-nerved, sub-bilabiate, 5-dentate; teeth lanceolate, the three posterior slightly shorter. *Corolla-tube* up to 9 mm. long, exterior pubescent, lobes rather small, about 1.5 mm. long, scarcely bilabiate. *Nucule* obovate, about 1.1 mm. long, deep purple-brown; areole \pm triangular, about $\frac{1}{3}$ as long as the nucule.

Distribution. Orient. S. ARABIA: Aden (*Thomson, Bayley Balfour, Beevor* 83, *Tehemsan Schweinfurth* 135, *Deflers* 21), Dhofar Mts., 2000 ft. (*Bent* 164).

Variation occurs in the density of indumentum of stem and leaf, and in the bract-length. *L. setifera* is easily distinguished by its long setaceous bracts forming tufts at the apex of young spikes, also by the stems, which are often terete, and by its characteristic leaves and habit; the bracts resemble those of *L. bipinnata* Kuntze var. *Rothiana* Kuntze, from which *L. setifera* is distinguished by its habit, leaves, and nucule characters.

*Explanation of the figures, wherein the numbers correspond
with those of the species in the paper.*

On p. 155.

Lower surface of leaf is shown, indumentum omitted. $\times 2$.

- 1, 1 a, *L. dentata* Linn.
- 17, 17 a, *L. somaliensis* Chaytor.
- 18, *L. pinnata* Linn. fil.
- 20, *L. Minutolii* Bolle.
- 21, *L. rotundifolia* Benth.
- 21 β , *L. rotundifolia* Benth. var. *subpinnatifida* Lowe.
- 21 γ , *L. rotundifolia* Benth. var. *crenata* Lowe.
- 27, *L. Nimmoi* Benth.
- 28, *L. setifera* Anders.

On p. 157.

Bracts and calyces shown at flowering stage: the marginal indumentum only is indicated. $\times 6$.

- 2, *L. Stoechas* Linn. *a*, calyx and corolla; *b*, fertile bract; *c*, sterile bract of coma.
- 3, *L. viridis* L'Hérit. Nucule.
- 4, *L. pedunculata* Cav. *a*, calyx and corolla; *b*, fertile bract; *c*, sterile bract of coma; *d*, nucule.
- 5, *L. officinalis* Chaix. *a, a*, bracts; *b*, nucule.
- 6, *L. latifolia* Vill. *a, a*, bracts; *b*, nucule.
- 7, *L. lanata* Boiss. *a*, dissected calyx; *b*, nucule.
- 23, *L. Gibsoni* Grah. *a*, bract; *b*, dissected calyx; *c*, nucule.
- 24, *L. bipinnata* Kuntze. *a*, nucule.
- 24 α , *L. bipinnata* var. *Burmanniana* Kuntze. *a*, bract; *b*, calyx.
- 24 β , *L. bipinnata* var. *Rothiana* Kuntze. *a*, bract; *b*, calyx.
- 24 γ , *L. bipinnata* var. *intermedia* Kuntze. *a*, bract; *b*, calyx.
- 25, *L. subnuda* Benth. *a*, bract; *b*, calyx; *c*, nucule.
- 26, *L. macra* Baker. *a*, portion of inflorescence; *b*, dissected calyx; *c*, nucule.
- 27, *L. Nimmoi* Benth. *a*, bract; *b*, calyx; *c*, dissected calyx.
- 28, *L. setifera* Anders. *a*, bract; *b*, calyx; *c*, dissected calyx.

On p. 159.

Bracts and calyces shown at flowering stage: the marginal indumentum only of bract and calyx is shown. $\times 6$.

- 8, *L. multifida* Linn. *a*, bract; *b*, calyx; *c*, portion of stem to show indumentum.
- 9, *L. Mairei* Humbert. *a*, bract; *b*, calyx.
- 10, *L. maroccana* Murb. *a*, bract; *b*, dissected calyx; *c*, nucule.
- 11, *L. canariensis* Mill. *a*, bract; *b*, calyx.
- 12, *L. Antineae* Maire. *a*, bract; *b*, calyx and corolla.
- 13 α , *L. brevidens* var. *ziziana* (Humbert) Maire. Dissected calyx.
- 13 β , *L. brevidens* var. *moulouyana* (Humbert) Maire. Dissected calyx.
- 13 γ , *L. brevidens* var. *mesatlantica* (Humbert) Maire. *a*, bract; *b*, dissected calyx.
- 14, *L. tenuisecta* Coss. *a*, bract; *b*, dissected calyx; *c*, nucule.
- 15, *L. pubescens* Dene. *a*, bract; *b*, dissected calyx; *c*, portion of stem to show indumentum.
- 16, *L. stricta* Del. Portion of inflorescence.
- 17, *L. somaliensis* Chaytor. *a*, bract; *b*, dissected calyx; *c*, calyx and corolla; *d*, nucule.
- 22, *L. atriplicifolia* Benth. Calyx and corolla.

A revision of the marine algae of Norfolk. By V. J. CHAPMAN, Ph.D., F.L.S.,

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(With PLATE 22, sketch-map, and 37 figures in the text)

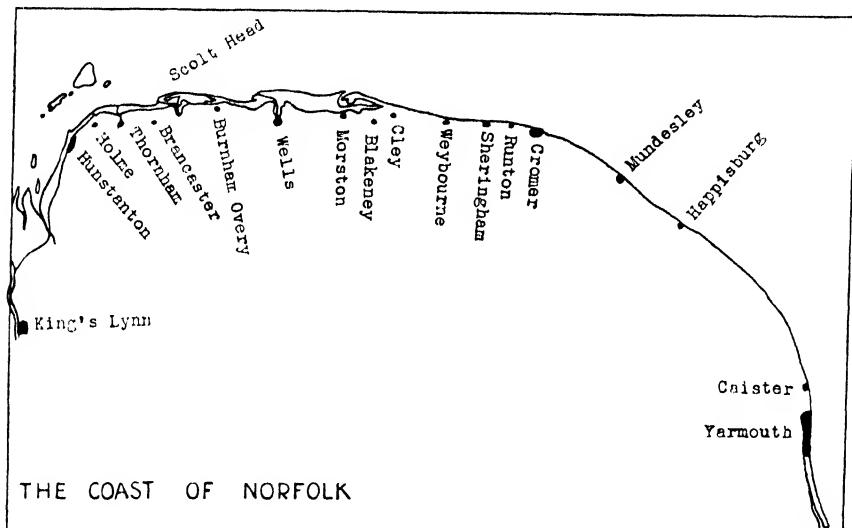
[Read 11 November, 1937]

THE last list of Norfolk algae to be published was that by H. D. Geldart (1883) in vol. III of the 'Transactions of the Norfolk and Norwich Naturalists' Society'. Since that date a few additions were noted by E. N. Bloomfield (1908) in the 'Transactions' of the same Society. The only subsequent lists are those by Cotton for Blakeney Point in 1929 and by the present author for Scolt Head in 1934. During the last four years the area between Holme and Mundesley has been worked very thoroughly by the author; some help was given by Miss C. Dickinson of the Royal Botanic Gardens, Kew, during a week in the spring of 1932 and by a party of Cambridge students for a fortnight in the spring of 1935. As a result, a very large number of additional species and forms have been found, and it is felt desirable that a new list should be published. It is clear from the earlier papers that the records were made mainly between Sheringham and Cromer, but, now that the Hunstanton-Cley area has also been worked, the list will be much more representative of the county. The publication of this list may stimulate students and visitors to search for additional species, and more particularly to confirm certain records which are doubtful owing to the fact that only one record has been made or one plant only has been seen. The data concerning the distribution of the Runton-Cromer species are especially vague, and the co-operation of visitors in supplying more information would be of great value.

The coast.—The area that has been laid under contribution is that part of Norfolk stretching from Hunstanton to Cromer. Admittedly, this is only about half the Norfolk coast-line, but it is doubtful whether any additional species would be recorded between Lynn and Hunstanton. It is possible that an examination of the coast between Waxham and Caister might result in the addition of a few more species. This is suggested by the fact that there are certain records which come only from Yarmouth, and these species may extend up to this part of the Norfolk Coast. This part of Norfolk is represented solely by the Yarmouth records.

Compared with a rocky coast, such as that of Cornwall or the Isle of Man, the Norfolk Coast should be poor in species. In actual fact, however, the total list numbers about 295, whilst the published lists for the Isle of Man include about 400 species. The principal reason for this large number is the

presence of a wide stretch of salt marshes that carry a peculiar algal flora which is rich in species, varieties, and forms. The area from Lynn to Cley is mainly that of salt marshes, although there is no large extent of natural marsh between North Wootton and Thornham. At Hunstanton there is an outcrop of sandstone and chalk, but there are only a few pools on the beach and no real boulders, and such algae as are found have nearly all been washed up. At Thornham there is a large extent of salt marsh, which forms a rich hunting ground. In addition, the main channel has a shingle bed, and here a number of species occur. Between Thornham and Brancaster there is a peat bed on the foreshore which is exposed at low-water. This also is a fairly rich ground for algae, especially for some of the Rhodophyceae. Another marsh area is reached at Brancaster Staithe, and this extends to Burnham Overy.



In addition to the mainland marshes there are also those of Scott Head Island. A rich algal area is provided by Norton Creek (the main creek between the island and the mainland) at the Brancaster end. Here the tide flows over a stony bed and the presence of mussel-lays has induced a very rich flora to develop. Where this creek joins the main harbour there is a shingle spit which has provided some species which are rare in this area. At the other end of the island is the breakwater in Burnham Overy harbour and this again is a rich locality, but the chief interest lies in the luxuriance of the plants which far excel those of any rocky coast area. A similar condition is found at Blakeney and has been commented upon by Cotton (1929). North of Scott Head and about half a mile off-shore there is a large flint-bed and here many species grow which can only be obtained by dredging or as cast-ups.

From Burnham Overy to Wells the coast is composed of sand-dunes and

'inned' marshes, and as such has no interest algologically. At Wells the greatest stretch of marsh begins and continues to Blakeney. These marshes are everywhere rich with algae, and at Blakeney there are additional species which grow in the main channel. It must be clear that the chief interest of this coast, algologically, lies in the marsh species, which are not to be found on a rocky coast. One may regard the algal flora of Norfolk as being complementary to that of a rocky coast and vice versa.

At Cley the nature of the coast changes, and from here to Weybourne there stretches a big shingle beach which physiographically is part of the Blakeney bank. Between Sheringham and Mundesley there are the chalk cliffs of Cromer and the beach is built of chalk. The Cromer area, therefore, differs considerably from the marsh area farther west, and it is found that the algal flora also changes. Many species have been washed up repeatedly at Runton and Cromer, indicating that there must be a bed off-shore similar to that off Scolt Head Island *. From Mundesley to Yarmouth the coast becomes flat again, and so far as the present paper is concerned it is unexplored. The ordnance survey map, however, shows a sandy beach with a row of dunes behind.

Algologically the coast may be divided into two areas: the marsh-coast, stretching from Lynn to Blakeney (except for the Hunstanton cliffs), and the cliff-coast, which extends from Weybourne to Mundesley.

The salt-marshes.—It has already been stated that the principal interest of the Norfolk algae is to be found in the salt-marsh species, and therefore it is essential that an adequate description of the marshes should be given. The marshes commence their development as bare sand- or mud-flats. The algal flora of the sand-flats is meagre, only a few species being found, e.g. *Enteromorpha compressa* f. *complanata*, *E. torta*, *Rhizoclonium implexum*, and often these are rolled together to form ropes. Where the substrate is mud, particularly a soft mud, then a rich algal community develops characterized by *Cladophora fracta*, species of *Enteromorpha*, *Asperococcus fistulosus*, *Monostroma Grevillei*, and *Fucus vesiculosus* var. *evesiculosus*. This community is so characteristic, being nearly always associated with beds of *Zostera nana*, that it is called the Muddy Chlorophyceae community (see p. 212). Sooner or later the sand- and mud-flats are invaded by plants of *Salicornia* spp. (samphire) and the algal vegetation changes. Growing between the *Salicornia* plants are to be found the thalli of the embedded fucoid, *Fucus vesiculosus* ecad *caespitosus*, whilst lying among the plants one finds *Pelvetia canaliculata* f. *libera*. Once the phanerogams have become established the marsh grows in height fairly rapidly and *Aster Tripolium* invades it. At this stage creek-formation begins and continues. On such low marshes the bed of the creek is either sandy or stony. If it is sandy it bears no permanent flora, whilst if it is stony then a definite flora will be found.

* Flint beds are exposed at low water between Sheringham and Cromer, and these bear a fairly rich flora.

On the higher marshes the creeks usually have a muddy or sandy bottom, and the algal flora is confined to the banks. Here a well-marked community is to be found, consisting mainly of Cyanophyceae. The dominant chlorophycean species is *Vaucheria Thuretii* which covers large areas, and is a primary colonist. It also plays a considerable part in binding the mud—a phenomenon obvious when one tries to remove some of the plants.

One of the characteristic features of the Norfolk marshes becomes evident on the low *Aster* marshes. This is the fringe of *Obione portulacoides* along the banks of the creeks. As the marshes increase in age so the *Obione* fringe becomes larger and forms a community, or *Obionetum*. Probably because the *Obione* bushes bring about peculiar conditions there is a definite algal flora associated with them. It is poor in species but they can be found nearly everywhere that an *Obionetum* occurs. The species concerned are :—

<i>Catenella repens.</i>	<i>Calothrix pulvinata.</i>
<i>Bostrychia scorpioides.</i>	<i>Phormidium corium.</i>
<i>Enteromorpha prolifera f. tubulosa.</i>	— <i>papyraceum.</i>
— <i>clathrata f. prostrata.</i>	— <i>autumnale.</i>
— <i>minima</i> (edges of creeks only).	

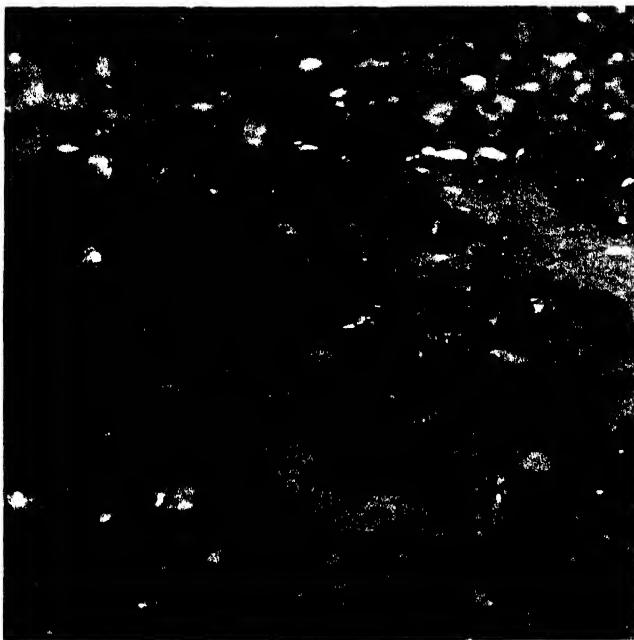
Along the edges of large creeks a form of *Aster* marsh is found which has been named the Creek-*Asteretum*. The normal *Aster* marsh is characterized by an almost pure algal community of *Bostrychia scorpioides*, and *Pelvetia canaliculata f. libera*. In the Creek-*Asteretum* the *Pelvetia* disappears and its place is taken by the marsh forms of *Fucus vesiculosus* (ecads *volubilis* and *caespitosus*), and other members of the genus *Enteromorpha* become common, especially *E. minima* which clothes the *Aster* stems.

With increasing height the *Aster* marsh gives way to a community known as the General Salt marsh. The number of algae here are fewer, but there is a definite autumn Cyanophyceae population.

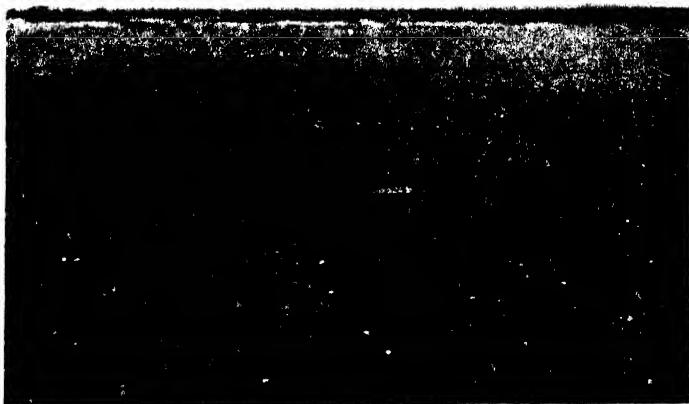
The algae show little change on the next two highest phanerogamic marsh communities which have been termed the Sea Meadow and *Plantagetum* respectively. The latter is interesting as on Scolt Head and at Brancaster Staithes it is the community in which *Fucus vesiculosus* ecad *muscoidea* is to be found growing as a moss-like turf (photo on Plate 22).

One of the highest communities for the area is the *Juncetum*, dominated by *Juncus maritimus*. The algal flora here is different, probably because of changes in the environmental conditions. A common species is *Vaucheria coronata*, and locally one may find patches of *Enteromorpha clathrata f. prostrata*. The bulk of the ground appears bare of algae, but if examined microscopically it will be found to have a rich flora of Cyanophyceae. Species recorded from the *Juncetum* of Scolt Head Island are :—

<i>Oscillatoria corallinae.</i>	<i>Chroococcus turgidus</i> var. <i>maximus</i> .
— <i>nigroviridis</i> .	<i>Nostoc Linckia</i> .
— <i>margaritifera</i> .	<i>Anabaena variabilis</i> .
— <i>laetevirens</i> .	<i>Rivularia atra</i> .
<i>Spirulina major</i> .	



1



2

John Bach, Scott & Curwen Ltd London

1. FLINT ROCK POOL AT SHERINGHAM.
2. HIGH MARSH ON SCOLT HEAD ISLAND.

In addition to those phanerogamic communities described above there are others, but they do not bear an algal flora characterized in any particular way, and so need not be specifically described.

The salt-pans.—All the marshes, from the *Aster* stage upwards, have salt-pans varying in size, shape, and depth. Two types of salt-pan can be distinguished, those with soft and those with hard floors. In general the soft-floored type are bare of algal vegetation, but, if they do have any, it is confined mainly to the edges and is peculiar. At Thornham and Wells there are a few pans of this type, and they contain the following species :—

Polysiphonia fibrata.

Colpomenia sinuosa.

Striaria attenuata.

Sphaerelaria radicans.

Vaucheria dichotoma var. *submarina* (also

at Burnham Deepdale).

Spirulina subsalsa.

Myriotrichia filiformis.

The species are all growing in these pans ; they are attached and, in general, appear healthy. They are also present in abundance. It is, however, most unusual to find such species growing in this type of habitat. The pans in question all occur on high-marshes when flooding will be very infrequent, especially in summer ; the water-supply is limited, and also it is stagnant. The species listed above are usually associated with a rocky coast and much water movement. The fact that the plants can and do thrive in the pans is a phenomenon that demands investigation. Such an inquiry would be expected to throw some light on the physical and environmental conditions which these algae are capable of tolerating.

When the flora of the firm-floored pans is studied it is noticeable that it may change to some extent with distance from the nearest large main channel, and also with height. The result is that the flora of pans on high marshes is meagre, whilst on low marshes and near main channels it is very rich. At least one author, Carter, has come to the conclusion that there is no true salt-pan flora. To anyone who has studied this part of the Norfolk coast intensively there is no doubt as to the existence of a salt-pan flora. The freshness of the plants and their continual presence throughout the year indicate that they are true inhabitants of the pans. Further, there are those plants already mentioned growing attached in the pans at Thornham and Wells, species which do not grow elsewhere in the area and which cannot, therefore, have been washed in. Even if they had been washed in it would be necessary to explain why they are confined to two pans at Thornham and six at Wells. Furthermore, if the pan flora is studied throughout the year it will be found that many of the species reproduce, especially species of *Monostroma* and *Cladophora*. The mere fact that these plants reproduce year after year indicates that they are leading a normal healthy existence, a view confirmed by the luxuriance of the individual specimens. It is worth noting in this connexion that Rees (1935) has also distinguished a pan flora from the marshes of Lough Ine. In addition to the Chlorophyceae of the pans there are a number of Cyanophyceae which become prominent in the autumn, mainly species

of *Lyngbya*. In investigating the salt-pan flora of low marshes one has to be careful in distinguishing between the indigenous flora and the 'cast-up' flora. This can only be done really satisfactorily by a long-period investigation such as the present one. Some help can also be obtained from the state and nature of the plants. In general, members of the Rhodophyceae can be regarded as 'cast-ups' and also most Fucaceae.

So far as the actual environment is concerned, the pans offer better conditions for the growth of algae than the marsh. They contain water long after the marsh itself is dry, and during spring tides this water is changed twice daily. In summer the pans certainly dry out, especially on the high marshes, but they dry out long after the surrounding marsh has become dry. Under these circumstances, therefore, it might be regarded as more unusual to find the pans bare of algae. The pan algae recorded for the marshes between Thornham and Blakeney are as follows :—

<i>Enteromorpha torta.</i>	<i>Striaria attenuata.</i>
— <i>intestinalis</i> f. <i>microphylla</i> .	<i>Sphaelaria radicans.</i>
— — f. <i>tubulosa</i> .	<i>Ectocarpus confervooides.</i>
— <i>prolifera</i> f. <i>tubulosa</i> .	<i>Myriotrichia filiformis.</i>
— <i>clathrata</i> f. <i>foeniculacea</i> .	<i>Bostrychia scorpioides.</i>
<i>Rhizoclonium implexum.</i>	<i>Polysiphonia fibrata.</i>
<i>Urospora isogona.</i>	<i>Microcoleus chthonoplastes.</i>
<i>Ulothrix speciosa.</i>	<i>Chrococcus turgidus</i> var. <i>maximus</i> .
— <i>subflaccida</i> .	<i>Lyngbya aestuarii.</i>
<i>Percursaria percusa.</i>	— — var. <i>spectabilis</i> .
<i>Monostroma orbiculatum.</i>	— <i>confervooides</i> .
— <i>crepidinum</i> .	— <i>majuscula</i> .
— <i>Wittrockii</i> .	<i>Spirulina subsalsa.</i>
<i>Cladophora fracta</i> var. <i>flexuosa</i> .	<i>Oscillatoria corallinae.</i>
— <i>expansa</i> .	— <i>sancta</i> .
<i>Vaucheria sphaerospora</i> var. <i>dichotoma</i> .	— <i>margaritifera</i> .
<i>Pelvetia canaliculata</i> f. <i>libera</i> .	— <i>laetevirens</i> .
<i>Fucus vesiculosus</i> ecad <i>volubilis</i> .	<i>Phormidium coriun</i> .
— — ecad <i>caespitosus</i> .	<i>Rivularia atra</i> .
<i>Acinetospora pusilla</i> var. <i>crinita</i> .	<i>Calothrix pulvinata</i> .
<i>Colpomenia sinuosa</i> .	

The main channels.—The main channels at Blakeney, Brancaster, Thornham, and Wells bear a rich flora the presence of which is dependent upon the stones and the usual mussel beds. The following species of Rhodophyceae are to be found here growing in pools or in the drainage streams :—

<i>Gracilaria confervooides.</i>	<i>Polyiphonia urceolata.</i>
<i>Polyiphonia nigrescens.</i>	— <i>elongata</i> .
<i>Ceramium rubrum.</i>	— <i>nigra</i> .
<i>Callithamnion byssoides</i> .	<i>Ceramium arborescens</i> .
— <i>Hookeri</i> .	— <i>tenuissimum</i> .
— <i>roseum</i> .	<i>Erythrotrichia carnea</i> .
— <i>polyspermum</i> .	<i>Achrochaetium virgatum</i> .
<i>Dumontia incrassata</i> .	<i>Laurencia hybrida</i> .
<i>Porphyra umbilicalis</i> var. <i>vulgaris</i> .	

The Chlorophyceae of these areas are numerous and include :—

<i>Ulva Lactuca</i> var. <i>latisima</i> .	<i>Cladophora sericea</i> .
<i>Enteromorpha intestinalis</i> f. <i>flagelliformis</i> .	<i>Cladophora gracilis</i> .
— <i>procera</i> .	— <i>rupestris</i> .
— <i>prolifera</i> f. <i>trichodes</i> .	— <i>flexuosa</i> .
— <i>intestinalis</i> f. <i>genuina</i> .	<i>Ulothrix flacca</i> (vernal only).
— <i>compressa</i> .	<i>Chaetomorpha melagonium</i> .
— <i>prolifera</i> f. <i>capillaris</i> .	<i>Bryopsis hypnoides</i> .
— <i>crinita</i> .	<i>Gomontia polyrhiza</i> .
— <i>minima</i> .	<i>Ulva Linza</i> .
	<i>Monostroma Grevillei</i> (vernal only).

Ulva is usually present in very large quantities, and in late summer and autumn numerous plants are torn from their anchorage and washed up on to the marshes.

The Phaeophyceae of such creeks include :—

<i>Elachista fucicola</i> .	<i>Fucus vesiculosus</i> var. <i>divaricatus</i> .
<i>Dictyota dichotoma</i> (summer).	— — var. <i>sphaerocarpus</i> .
<i>Pylaiella littoralis</i> .	— <i>spiralis</i> var. <i>platycarpus</i> .
<i>Ectocarpus confervoides</i> .	— <i>serratus</i> .
— <i>siliculosus</i> .	<i>Chorda Filum</i> (aestival).
— <i>tomentosoides</i> .	<i>Laminaria saccharina</i> .
— <i>Hincksiae</i> .	<i>Asperococcus fistulosus</i> .
<i>Ralfsia clavata</i> .	<i>Phyllospadix Fascia</i> (vernal).
<i>Myriophyllum strangulans</i> .	<i>Pelvetia canaliculata</i> .
<i>Fucus vesiculosus</i> .	

The escarpments.—Where the large creeks run through the marshes a steep cliff is often found (locally known as 'Mud Steeps') where the marsh has been eroded. These vertical cliffs bear a characteristic algal vegetation, mainly Cyanophyceae, and, in particular, species of *Oscillatoria* and *Phormidium*, *Spirulina subtilissima*, *Rivularia atra*, *Calothrix scopulorum*, and *C. pulvinata*. The community is so characteristic that it has been termed the Marginal Cyanophyceae.

Other places of interest.—Sluices where 'inned' marshes have their drainage outlet are always worth investigation. Interesting ones are those at Thornham and Burham Deepdale.

Another place of interest is where fresh water is flowing out to sea, such as in Thornham and Blakeney main channels. Here one may get such species as *E. intestinalis* f. *maxima*, *E. procera* f. *maxima*, and *E. intestinalis* f. *Cornucopiae*.

ECOLOGY.

One of the most attractive features of the salt-marsh algal vegetation is its ecological aspect. The species form a number of well-marked communities, which can be readily recognized in the field. Some of these communities have already been recognized and described from other salt-marsh areas, but some are recorded here for the first time. It is only proposed in this paper

to give a brief outline of these algal communities. The first group to be considered is termed the General Chlorophyceae association, and it is subdivided into three communities. Cotton (1912) in the Clare Island Survey recognized four communities, but did not group them together into an association. Carter (1933) in the work on the Canvey and Dovey marshes found that there was no real distinction between the communities and so she only described one association.

General Chlorophyceae Association :—

(a) Low Sandy Chlorophyceae. This is the community dominated by *Enteromorpha prolifera* f. *capillaris*, with *Vaucheria Thuretii* and *E. intestinalis* f. *flagelliformis* associated with it. It is common on soft sand and muddy sand in large creeks. The *Vaucheria Thuretii* community on the banks of large creeks may be regarded as a subdivision.

(b) Sandy Chlorophyceae. This is a large community, and probably the least satisfactory because of its great variation. It is usually dominated by either *Enteromorpha torta* or *Rhizoclonium implexum* or both. It contains a number of Cyanophyceae which are mainly confined to high marshes, whilst some members of the Chlorophyceae, *Monostroma* spp., *Vaucheria sphaerospora*, and *V. coronata* may be locally sub-dominant. As a community it is the most widespread and can be found on all marshes from the lowest sand-flat to the highest marsh.

(c) Muddy Chlorophyceae. This community is restricted to soft-mud areas, especially where *Zostera nana* is growing. It has been seen on Scolt, Morston, and Blakeney marshes where it occupies considerable areas. It is characterized by the presence of *Cladophora* spp., by *Asperococcus fistulosus*, *Phyllitis Fascia*, and *Monostroma Grevillei* in the spring, by *Fucus vesiculosus* var. *vesiculosus*, *Pylaiella littoralis*, and *Ectocarpus confervoides* which persist throughout the year.

Marginal Cyanophyceae community.

This is found on the vertical banks of large creeks and also on the horizontal banks in the creeks. The dominant species are Cyanophyceae, which have already been mentioned (cf. p. 211).

Ulothrix community.

This is principally a vernal community, and has a wide distribution. The dominant species on the coast may be *Ulothrix speciosa*, *U. implexa*, or *Urospora isogona*. It is found growing on the stones in the beds of small creeks, over the vegetation on low marshes, and frequently filling pans with a mass of silky green threads. The silky nature of the threads when pulled apart in the field enables this community to be readily recognized.

Enteromorpha minima community.

A very common community on low marshes and on the *Obione* bushes fringing the creeks. In most cases *E. minima* is the only species present.

It is very abundant in spring when it clothes the old stems of *Aster* plants with a green blanket; and in the summer it forms a coating on the *Obione* bushes. Occasionally it may be found on the open marsh, especially in winter when *E. minima* grows epiphytically upon the dead leaves of *Limonium vulgare* on low marshes.

Gelatinous Cyanophyceae community.

The name given to this community is based upon the nature of the dominant species, *Nostoc commune*. So far, this community has only been recorded from Scolt Head Island, but it probably will be found also at Blakeney. It frequents the edges of old shingle laterals on high marshes and may also be found in lows.

Autumn Cyanophyceae community.

This is a very striking community, which exists only during the autumn months, although isolated specimens of the component species may be found at all times of the year. It occurs on all high marshes, covering the bare ground with a grey blue felt, and is particularly abundant in the pans of the upper marshes. A feature which seems peculiar to Norfolk is the abundance of *Chroococcus turgidus* var. *maximus*.

Phormidium autumnale community.

A community confined almost entirely to the *Obionetum* fringing the large creeks. In some places the blue-green sheets are very conspicuous, especially in the autumn months. *P. autumnale* is the dominant species, but is usually associated with *P. corium* and *P. papyraceum*. *Calothrix pulvinata* may be locally abundant, growing epiphytically on the stems of the *Obione* bushes.

Rivularia-Phaeococcus community.

A community which has been described for the vertical banks of marshes in Ireland, but which in Norfolk grows on the flat marsh (cf. p. 257).

Catenella-Bostrychia community.

Cotton has stated that long exposure to air is a characteristic of the community and in general this holds true in Norfolk (cf. p. 261).

Pelvetia-Bostrychia community.

This community is described here for the first time and there is no doubt that it is characteristic of the Norfolk marshes, for it can be found from Thornham to Blakeney. It attains its maximum development in *Aster* marshes, but may occur on marshes lower or higher. In places, only one of the dominant species may be present, but generally both occur. It is interesting to record that at Thornham *Bostrychia scorpioides* is by far the most abundant, whilst at Scolt and Blakeney *Pelvetia canaliculata* f. *libera* is the more frequent. On high marshes the *Pelvetia* plants show considerable stunting and usually *Enteromorpha prolifera* f. *tubulosa* plays a greater part. *Bostrychia scorpioides* occurs over the whole range of the community and therefore is probably more tolerant towards the environmental conditions.

Enteromorpha clathrata community.

The dominant species here is *E. clathrata* f. *prostrata*. This is another community which is described for the first time, and it is abundant on high marshes all along the Norfolk coast. It probably occurs also on the Essex marshes, as the dominant species was found on a recent visit to the marshes of Hampden Water and Mersea Island.

Fucus limicola community.

This exists in three separate facies depending on the dominant species, which may be *Fucus vesiculosus* ecads *volubilis*, *caespitosus*, or *muscodoides*.

Pan community.

This community has already been discussed at some length and the species recorded in full (cf. p. 210).

FACTORS CONTROLLING ALGAL DISTRIBUTION.

As yet comparatively little work has been done on the factors which determine algal distribution, especially on a salt-marsh coast. Johnson and Skutch (1928), Klugh (1924), Knight (1931), and Baker (1909) have carried out a certain amount of work on the distribution of algae on a rocky coast, but the conditions on such a coast are, in many respects, very dissimilar to those existing on a marsh coast, and it is not safe to argue from one to the other. It may be of service if an outline is given here of the principal factors which appear to be operating on salt marshes in so far as the algae are concerned :—

(i) *Submergence and emergence*.—The principal factor on any shore must be the tides which operate in covering the vegetation daily, or at certain periods only, depending upon the level. At any given level there will be a certain number of submergences *per annum* and a complementary number of exposures. In the case of some algae there may be a limit to the number of exposures which the species can endure or a limit to the number of submergences. The upper limit of *Peltvetia canaliculata* f. *libera* may be determined by exposure, a suggestion based upon the stunted growth of the alga on high marshes and its general restriction to salt pans in such areas. *Vaucheria coronata* is an alga which is confined to one of the highest zones on the marshes, and its downward spread may be limited by the number of submergences which it can endure. In this case there is no information available to support the hypothesis. So far as the algae are concerned, this factor is probably not of such great significance as it is to the phanerogams.

(ii) *Periods of non-tidal exposure*.—By the term *non-tidal* exposure is meant the consecutive days during which no tide covers the area. The period between two successive tides is known as the *inter-tidal* exposure. Non-tidal exposure is probably of great importance in determining algal distribution. For any given level there is a maximum period for a single exposure, and on high marshes this may be as much as 84 days. Owing to the nature of the

tides along this coast, there are relatively small spring tidal rises in summer, and so high marshes may be exposed for long periods in that season. During such an exposure the only source of moisture is rainfall and dew. In many marsh areas of England this may be considerable during the summer, but it so happens that the marsh coast of Norfolk is exceedingly dry. The algae on the high marshes are therefore exposed to considerable desiccation. It is the degree of desiccation which a species can tolerate that probably determines in many cases its upper limit. This must particularly be the case for the more delicate species, e.g. most members of the Chlorophyceae. If a list be made of species occupying high marshes it is found that nearly all these are Cyanophyceae (which are known to be able to withstand drought) or are certain Phaeophyceae which also can endure considerable exposure. In the summer the surface algae (Chlorophyceae) are bleached, and the living threads lie underneath the whitened mass. It is from these protected threads that new filaments develop in the autumn.

(iii) *Temperature*.—This factor operates on high and low marshes, but in rather different ways. On high marshes temperature may be of great importance in causing desiccation during the summer months when the marshes may be dry for a long time. On low marshes the ground tends to become heated during the day and in alternate weeks it becomes flooded in the afternoon or evening by the relatively cold sea-water. This induces a sudden change of temperature which Johnson and Skutch (1928) have demonstrated as an important factor in determining the algal vegetation of rock pools. Knight and Parke (1931) have also emphasised the importance of temperature in determining the zonation on a rocky coast. They consider that it is partly responsible for the vertical migration of some species: vertical migration has not been observed along the Norfolk coast, but such observations would be difficult in any case because the zones (such as they are) are separated by large horizontal distances.

(iv) *Salinity*.—It is not impossible that the distribution of some algal species may be determined, wholly or partly, by the degree of salinity which they can tolerate. In so far as salinity is concerned it may be either the maximum or minimum degree of salinity in an area which is the limiting factor, or it may be the maximum range of salinity in the area which is decisive. Field experiments and estimations will be the principal means of distinguishing between these two possibilities. In the summer it is obvious that the surface of the soil on high marshes must reach a very high degree of salinity because a crust of salt is deposited and actually may cover the algae. The high summer salinity may effectually prevent the upward migration of some algae. Baker (1912) has suggested that it may be one of the factors determining some of the features of the marsh fucoids, such as spirality of the thallus.

(v) *Light*.—Klugh (1924) has shown that the light supply may be of importance in relation to the algae, and it has been suggested earlier that

the colour of *Catenella repens* may be determined by the light intensity. The distribution of red and brown algae may be determined by this factor, as also may be the lower limit for some of the Chlorophyceae. Low marshes may be covered by a considerable depth of water fairly frequently and for quite a long period at a time. The depth of water must cut off the light supply and may do so to a limiting extent.

(vi) *Substrate*.—It has been suggested that this may be of importance in determining the distribution of the Muddy Chlorophyceae community. In a more general way it divides Norfolk into two areas: the salt marsh area where the substrate is not solid and the Cromer area where the substrate is solid chalk rock. This difference of substrate is responsible for the richness of the Norfolk flora as a whole.

(vii) *Current*.—This factor limits the distribution of species which thrive best in well-aerated conditions, and as a consequence such species will be confined to the beds of main channels and large creeks. Because of the swiftness of the current it is noticeable that between Thornham and Blakeney the algae living in the main channels attain to a luxuriance that is comparatively unknown on a rocky coast.

(viii) *Wave action*.—This factor is of principal importance in the Cromer area, and coastal erosion is actually taking place. Wave action and concomitant erosion prevent the development of a rich flora. The same process, in miniature, is taking place on the salt marshes where only a few species can grow on the vertical banks of creeks, and these are liable to be washed away at any time. Erosion of salt marsh 'steeps' depends on the direction of the wind and the extent of open water over which it is blowing. Much of the erosion seems to be brought about by water draining back into the creek over the edges after a flooding tide.

(ix) *Phanerogams*.—It is doubtful how far these determine algal distribution, except in so far as they may determine some of the environmental conditions, especially humidity, light, and shade. Bushes of *Suaeda fruticosa* and *Obione portulacoides* may provide sufficient shade and humidity on high marshes for certain species to grow under them, whereas on the open marsh the same species would not survive.

(x) *Biota*.—This is the expression of the competition of one species with another or the effect of animals upon the algae. Of the fauna the only species which is present in sufficient number to influence the distribution of algae is *Hydrobia ulvae*, a small mollusc. This is present in vast quantities on low marshes and feeds mainly on Chlorophyceae, especially species of *Ulva* and *Monostroma*. The number of *Hydrobia* may possibly be the factor preventing the downward spread of species of *Monostroma* to low marshes, since they are readily attacked. On high marshes the *Hydrobia* are less numerous and the *Monostroma* spp. thrive. The most striking example of successful

competition among algae is provided by the *Pelvetia-Bostrychia* community, the plants of which may be so numerous as to prevent any other species growing in the area.

Finally, it may be noted that along the Norfolk coast some species appear to be sublittoral, whereas on rocky coasts they are littoral, and with other species the reverse is the case. The first of these phenomena may be due to the fact that there are no rock pools or crannies in which delicate forms can grow during the period of low tide, and so such forms have become sublittoral. The reason for the reverse phenomenon is to be found in the presence of the channels, such as those of Thornham, Brancaster, Burnham Overy, Wells, and Blakeney. At low water these always have a stream of drainage and spring water, even though there is no tide, and this permanent water enables sublittoral species to grow at levels considerably higher than low-water mark. The fact that these differences in distribution can be recorded should provide a clue towards indicating the conditions under which certain species will survive. The species, which along the Norfolk coast are sublittoral, but which on rocky coasts are littoral, may be assumed to have no tolerance towards exposure, such exposure operating through desiccation or changes of salinity. The following species on the Norfolk coast occur at a lower level than they do on a rocky coast such as Port Erin:—

Species.	Level in Norfolk.	Level at Port Erin.
<i>Enteromorpha compressa</i>	M.T.-L.W.O.S.T.	H.W.O.S.T.-M.T.*
<i>Cladophora pellucida</i>	Sublittoral.	M.T.-L.W.O.N.T.
<i>Chaetopteris plumosa</i>	Sublittoral.	L.W.O.N.T.
<i>Cladostephus verticillatus</i>	Sublittoral.	M.T. downwards.
<i>Pelvetia canaliculata</i>	H.W.O.N.T.	H.W.O.S.T.
<i>Acrochaetium endozoicum</i> ...	Sublittoral.	L.W.O.S.T.
<i>Chondrus crispus</i>	Sublittoral.	M.T. downwards.
<i>Phycodrys rubens</i>	Sublittoral.	L.W.O.N.T.-L.W.S.T.
<i>Hypoglossum Woodwardii</i> ...	Sublittoral.	M.T.-L.W.O.S.T.
<i>Griffithsia flocculosa</i>	Sublittoral.	M.T. downwards.
<i>Furcellaria fastigiata</i>	Sublittoral.	M.T. downwards.
<i>Cruoriella Dubyi</i>	Sublittoral.	M.T. downwards.

In contrast to this there are those species which occur at a higher level on the Norfolk coast than on a rocky coast. Their presence may, in many cases, be due to the salt pans holding water. As these often dry out in summer, it suggests that such species can tolerate occasional exposure to desiccation

* L.W.O.S.T.=Low-water ordinary spring tide.

H.W.O.S.T.=High-water ordinary spring tide.

L.W.O.N.T.=Low-water ordinary neap tide.

H.W.O.N.T.=High-water ordinary neap tide.

M.T.=Mid-tide.

and changes of salinity. These species may be divided into three groups in respect of their occurrence on the marsh coast :—(A) those occurring in pans ; (B) those occurring in streams ; (C) those occurring on the marshes.

A.

Species.	Level in Norfolk.	Level at Port Erin.
<i>Ulothrix flacca</i>	M.T.—H.W.O.N.T.	L.W.O.N.T.
<i>Striaria attenuata</i>	H.W.O.S.T.	Sublittoral.
<i>Colpomenia sinuosa</i>	H.W.O.S.T.	H.W.O.N.T.—L.W.O.N.T.
<i>Myriotrichia filiformis</i>	H.W.O.S.T.	M.T. and downwards.
<i>Sphacelaria radicans</i>	H.W.O.S.T.	M.T.

It is to be noted that on a rocky coast these species are usually to be found in rock-pools where the conditions will be somewhat similar to those of salt-pans. Their absence at higher levels on a rocky coast may be accounted for by the competition existing with other species. On the salt marshes the number of species at high levels are relatively few and small in size, whereas on a rocky coast they are abundant and often large, e.g. Fucaceae.

B.

Species.	Level in Norfolk.	Level at Port Erin.
<i>Chorda Filum</i>	M.T.	L.W.O.N.T. and below.
<i>Laminaria saccharina</i>	M.T. and below.	L.W.O.N.T. and below.
<i>Polysiphonia elongata</i>	M.T.	L.W.O.S.T. and below.
— <i>nigra</i>	M.T.	Sublittoral.
<i>Callithamnion byssoides</i>	M.T. and below.	L.W.O.S.T. and below.
— <i>roseum</i>	M.T. and below.	L.W.O.N.T. and below.

The reason for the existence of these species at high levels in Norfolk is probably to be sought in the presence of water which is continually in motion. These species probably require continual submersion by water (as is found also in salt pans) and good aeration.

C.

Species.	Level in Norfolk.	Level at Port Erin.
<i>Chaetomorpha litorea</i>	H.W.O.S.T.	L.W.O.N.T.
<i>Cladophora flexuosa</i>	H.W.O.N.T.	L.W.O.S.T.
<i>Catenella repens</i>	H.W.O.S.T.	M.T.

The explanation for the differences in level of these species is difficult to discover. The conditions of the marshes little resemble those of a rocky coast, and it is obvious that on a marsh the species must tolerate a greater exposure than they undergo on a rocky coast. It cannot be a question of water supply or aeration nor can it be humidity, because the upper littoral of a rocky coast is probably as humid as that of a marsh coast. A possible explanation seems to lie in the degree of competition, this being much less or even absent on a marsh coast.

THE ECOLOGICAL UNITS.

When the algal communities of the marshes were described no attempt was made to classify them ecologically, and they were regarded in general as communities, a term which involves no hard-and-fast significance. It is probably desirable, however, that some indication should be given of the way in which these communities should properly be regarded. Following the practice of a number of previous authors it is convenient to divide the coast into three major regions, each of which will have its formations, associations, societies, and clans. The regions are :—

- (1) Littoral. L.W.O.S.T. to the highest level attained by marine algae.
- (2) Sublittoral L.W.O.S.T. to 25 fathoms.
- (3) Elittoral. Below 25 fathoms.

Region (3) rarely has any interest algologically and none at all along the Norfolk Coast. Little can be said about region (2) since so few facts are known concerning the exact nature of the bottom off-shore. It may be suggested that two formations are possible along the Norfolk Coast, both of which are known to exist :—

- (1) Chalk Formation (off-shore at Scolt, Runton, and Cromer).
- (2) Peat-bed Formation (off-shore at Brancaster).

These may each have a distinct flora, but until more extensive dredging operations are undertaken no further information will be forthcoming.

Region (1) has been divided by previous authors into three formations and these are retained here :—

- (a) Rocky shore formation.
- (b) Sand and sandy-mud formation.
- (c) Salt marsh formation.

At present it is perhaps advisable to omit any very detailed elaboration of (a) until further information is available. On a rocky coast the shore level is stable, and as a result the algal zones are static and the whole formation can be regarded as a climax formation. On salt marshes and sand or sandy-mud areas there is the complication of growth in height of the shore, so that one algal community may eventually be replaced by another. In other words, the salt-marsh formation cannot be regarded as a climax formation. In view of the evidence that salt marsh probably develops into fresh-water bog there seems no reason to suppose that salt marshes ever have an algal climax formation upon them. On the other hand, conditions may be such that development into fresh-water marsh is impossible, in which case there may be a salt-marsh subclimax formation for the algae. The communities of the salt-marsh formation have already been described, and it merely remains to stress the fact that they are, in general, developmental, being dependent upon marsh level and the other factors mentioned previously.

Sand and sandy-mud formation.—This formation is encountered on the bare sand and mud flats of the salt-marsh area. It is composed of the General Chlorophyceae associes which contains two well-marked consocies:—

- (a) Muddy Chlorophyceae.
- (b) Low Sandy Chlorophyceae.

These generally develop into one of the salt-marsh communities.

Rocky coast formation.—A short survey of the coast at Hunstanton and between Overstrand and Weybourne enables one to suggest the principal consociations that may be encountered. At Hunstanton there is an upper *Enteromorpha-Fucus platycarpus* consociation with *E. compressa* f. *intermedia* as the co-dominant. Other common species are:—

<i>Ceramium flabelligerum.</i>	<i>Ulva Lactuca.</i>
<i>Cladophora sericea.</i>	<i>Callithamnion byssoides.</i>
<i>Pylaiella littoralis.</i>	<i>Cladophora glaucescens.</i>

In parts one of the co-dominants may form a society, whilst *Phormidium corium* forms an encrusting society on the boulders.

On the boulders near low-water mark and amongst the mussel beds another consociation can be distinguished dominated by *Fucus vesiculosus* var. *vesiculosus* and *E. compressa* f. *typica*. Additional species confined to this consociation are:—

<i>Ceramium rubrum.</i>	<i>Porphyra umbilicalis</i> var. <i>vulgaris</i> .
— <i>arborescens</i> .	<i>Pylaiella littoralis.</i>

In the Cromer area there appear to be two main associations, which are natural, and in addition the artificial consociation of the breakwaters. The latter is a *Fucus-Porphyra-Enteromorpha* consociation dominated by *Fucus platycarpus*, *Porphyra umbilicalis*, and *Enteromorpha compressa* f. *typica*. Other species are *E. micrococca* f. *tortuosa*, *Cladophora rupestris*, *Ulothrix flacca*, and *Rhodochorton Rothii*.

There is also an upper natural consociation between the high-water marks dominated by *Porphyra umbilicalis* and *Enteromorpha compressa* f. *typica*, but the subsidiary species are few in number and are not abundant. The two principal associations are (a) the Chalk beach association and (b) the Flint bed association.

More detailed investigation will probably show that these may have a number of subsidiary consociations. It is probable that at E. Runton there is a *Cystoclonium purpurascens* consociation and towards low-water mark there may also be a *Laurencia pinnatifida* consociation. *Corallina officinalis* forms a marked society in the pools, whilst *Cladostephus spongiosus*, *Pterosiphonia thuyoides*, and *Gelidium crinale* also form local societies. *Fucus serratus* dominates most of the chalk beach association, whilst *Fucus vesiculosus* is more abundant on the flint bed.

The Flint bed association appears to contain a consociation of the encrusting *Hildenbrandia prototypa*; and *Lithothamnion Lenormandi*. There is also a *Cladophora utriculosa* consociation near low-water mark, whilst *Gracilaria confervoides* often occurs locally in sufficient abundance to form a consociation. Other species of interest from the flints are :—

<i>Cystoclonium purpurascens.</i>	<i>Enteromorpha chartacea.</i>
<i>Chaetomorpha melagonium.</i>	<i>Pterosiphonia thuyoides.</i>
<i>Ceramium echionotum.</i>	<i>Cladophora rupestris.</i>

All these associations and consociations can be regarded as forming a static climax vegetation, because there is no fluctuation in level over a short period of time such as there is on the marshes.

THE FLORA LIST.

This has been compiled from previous lists, to which have been added the present author's own records. The previous lists used are those by Geldart (1882) (incorporating all earlier lists), Cotton (1929), Bloomfield (1908), and Newton (1931). Species that are regarded as uncertain are best omitted until such time as further records are available. Such an example is *Urospora collabens* recorded once on floating timber. There are also some records from Yarmouth which need further confirmation, and there is need of an investigator to work the Waxham-Caister area, because it will be there that new records of the Yarmouth species may be obtained. The species recorded from Yarmouth only are as follows :—

<i>Cystoseira discors.</i>	<i>Callithamnion fasciculatum.</i>
<i>Laminaria saccharina</i> var. <i>latissima</i> (cf. note 24, p. 262).	<i>Bangia fusco-purpurea.</i>
<i>Desmarestia aculeata.</i>	<i>Colacolepis incrassans.</i>
<i>Acrochaetium secundatum.</i>	<i>Prasiola stipita.</i>
<i>Callophyllis jubata.</i>	<i>Blastophysa rhizopus.</i>
	<i>Dermocarpa Schousboei.</i>

The list is based upon the classification used by Newton (1931) in the 'Handbook of British Seaweeds', since this is more recent than Harvey's 'Phycologia' (1849) or Batter's 'Catalogue' (1902). It is hoped that the information provided will be such as to enable future workers and naturalists to find the commoner species without much difficulty. The expression 'Cromer area' refers to the coast between Sheringham and Mundesley. Figures of most of the species listed can be found in one or more of the following works :— Rabenhorst (1885), Newton (1931), Carter (1933), Harvey (1849), and Heering (1921). References to the remainder occur in the text.

MYXOPHYCEAE.**CHROOCOCCACEAE.**

CHROOCOCCUS TURGIDUS Naeg., var. **MAXIMUS** Nygaard.

D.*—Thornham to Blakeney. Z.—High marshes. O.—Late summer and autumn. N.—Found in pans mixed with felts of *Lyngbya*, often in large quantities (cf. Note 1, p. 256).

APHANOCAPSA MARINA Hansg.

D.—Scolt Head. O.—Sporadic. N.—Epiphytic, rare, recorded from Overy End Marsh.

MERISMOPEDIA GLAUCA Kütz.

D.—Scolt Head. Z.—Edges of low marshes (*Salicornietum*). N.—Although originally described for fresh-water, this species seems to have a fairly wide marine distribution. Rare, only found once.

CHAMAESIPHONACEAE.

DERMOCARPA SCHOUSBOEI Born. : *Xenococcus Schousbei* Thur.

D.—Yarmouth. O.—Sporadic. N.—Epiphytic on small algae.

DERMOCARPA PRASINA Born.

D.—Scolt Head. Z.—High marsh. O.—Sporadic. N.—Rare. Only found once, on Great Plantago Marsh.

LYNGBYACAE.

SPIRULINA SUBSALSA Oerst. : *S. tenussiima* Kütz.

D.—Blakeney and Thornham. Z.—Low marshes. O.—All the year. N.—Forming a blue-green stratum on mud in or near pans.

SPIRULINA SUBTILISSIMA Kütz.

D.—Scolt Head. Z.—H.W.O.S.T. O.—Late autumn. N.—On the mud in the *Juncetum* and also on the escarpment of Norton Creek in its middle section.

OSCILLATORIA MARGARITIFERA Kütz.

D.—Scolt Head. Z.—Upper marshes. O.—All the year, more abundant in winter. N.—On the mud. Never very abundant. Sometimes frequent along the banks of the larger creeks. Probably distributed from Thornham to Blakeney.

OSCILLATORIA NIGROVIRIDIS Thwaites.

D.—Scolt Head. Z.—Middle and upper marshes. O.—All the year, more frequent in autumn. N.—On the mud of the marshes and in pans. Probably to be found from Thornham to Blakeney.

* D.=district, Z.=zone, O.=occurrence, N.=notes.

Oscillatoria corallinae Gom.

D.—Scolt Head. Z.—Middle and upper marshes. O.—Autumn. N.—On the mud banks of the larger creeks and on the marsh mud. Probably distributed from Thornham to Blakeney.

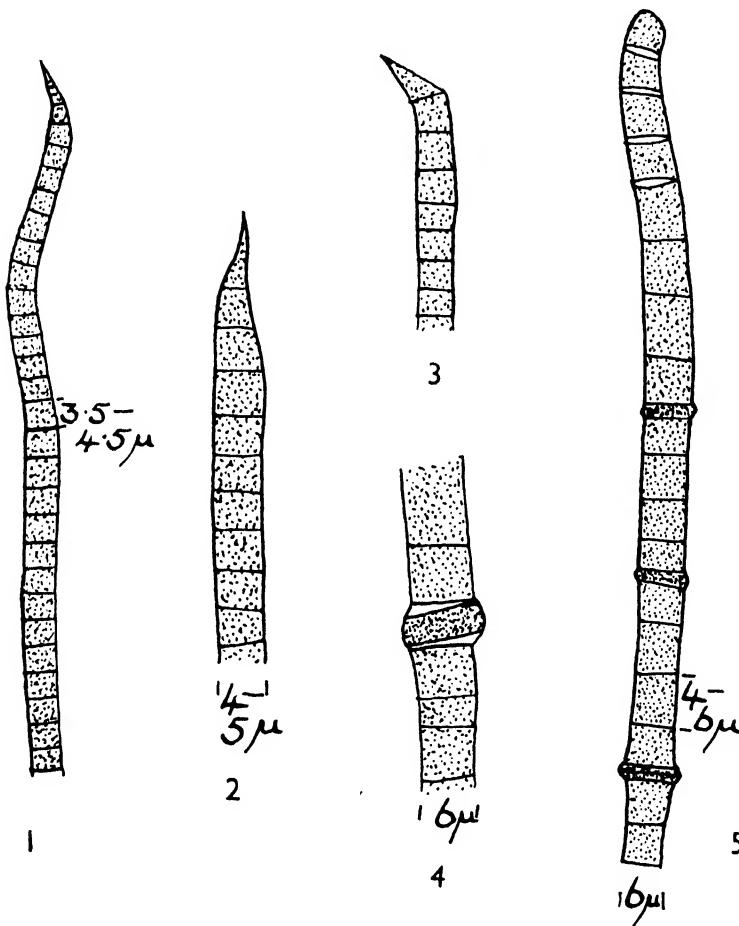


FIG. 1.—1-3, *Oscillatoria acuminata*; 4 & 5, *O. brevis* var. *neapolitana*.

Oscillatoria sancta Kütz.

D.—Scolt Head. Z.—Middle and upper marshes. O.—Autumn. N.—Probably distributed from Thornham to Blakeney on the mud banks of large creeks and on the marsh mud.

Oscillatoria limosa C. A. Agardh.

D.—Blakeney. N.—Common in pans and sometimes binding sand.

OSCILLATORIA LAETEVIRENS Crouan.

D.—Scolt Head. Z.—Middle and upper marshes. N.—Not a common species. Found mixed up with other Cyanophyceae on the mud banks of the larger creeks on the marsh mud and in pans.

OSCILLATORIA FORMOSA Bory.

D.—Scolt Head. Z.—Upper marshes. O.—All the year, but more frequent in the autumn. N.—Mixed with other Cyanophyceae on the mud banks of creeks and in pans.

OSCILLATORIA BREVIS Kütz. var. **NEAPOLITANA** Gom. (cf. Note 2 on p. 256).

D.—Scolt Head. Z.—Upper marshes in the *Obionetum*. N.—Very rare. Only found once.

OSCILLATORIA ACUMINATA Gom.

D.—Scolt Head. Z.—Upper marshes. N.—Very rare. Only found once (cf. p. 256, Note 3).

PHORMIDIUM CORIUM Gom.

D.—Scolt Head, Hunstanton. Z.—All marshes. O.—All the year, most abundant in autumn. N.—A frequent species, especially in the *Obionetum* and on the mud banks of large creeks. Probably widely distributed between Holme and Blakeney.

PHORMIDIUM TENUЕ Gom.

D.—Scolt Head. Z.—Upper marshes. O.—Late summer and autumn. N.—Generally mixed up with other Cyanophyceae.

PHORMIDIUM PAPYRACEUM Gom.

D.—Scolt Head. Z.—Upper marshes in the *Obionetum*. O.—Late summer and autumn. N.—Not common. Mixed up with other species of *Phormidium*.

PHORMIDIUM AUTUMNALE Gom.

D.—Scolt Head. Z.—Upper marshes in the *Obionetum*. O.—All the year, but most abundant in the autumn. N.—Forms a blue mat beneath the *Obione* plants in the late summer and autumn. As described by Carter in the 'Journal of Ecology' the calyptra was often absent. Probably distributed between Thornham and Blakeney.

LYNGBYA AESTUARII Liebm.

D.—Holme to Blakeney, Hunstanton. Z.—Upper marshes. O.—Late summer and autumn. N.—Forms the principal constituent of the grey-blue felt covering the soil of the upper marshes in autumn. Isolated threads can be found throughout the year.

LYNGBYA AESTUARII Liebm. var. **SPECTABILIS** Gom. : *L. spectabilis* Thur.

D.—Holme to Blakeney. Z.—Upper marshes. O.—Late summer and autumn. N.—Always found associated with the typical species from which it is distinguished by the yellow inner layer of the sheath (cf., however, Note 5 on p. 256).

LYNGBYA CONFEROIDES C. A. Agardh.

D.—Holme to Blakeney. Z.—Upper marshes. O.—Summer and autumn. N.—Mixed up with *L. aestuarii*.

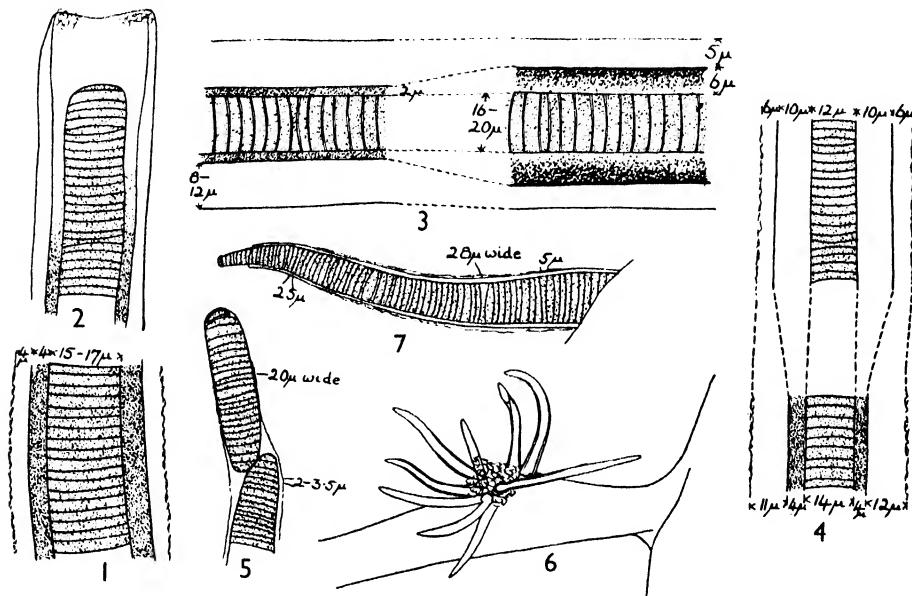


FIG. 2.—1-4, *Lyngbya aestuarii* var. *spectabilis*; 5-7, *Calothrix consociata*.
6, $\times 25$.

LYNGBYA MAJUSCULA Harv.

D.—Holme to Blakeney. Z.—Middle and upper marshes. O.—All the year. N.—Occurs sparingly in felts and floating in pans.

LYNGBYA SEMIPLENA J. G. Agardh.

D.—Holme to Blakeney, Hunstanton. Z.—Marshes. O.—All the year. N.—Occurs sparingly on the mud round the edges of marshes.

VAGINARIACEAE.**MICROCOLEUS CHTHONOPLASTES** Thur. : *M. anguiformis* Harv.

D.—Holme to Blakeney. Z.—All marsh levels. O.—All the year; most abundant late summer and autumn. N.—Distributed almost everywhere, particularly frequent around the edges of all marshes.

MICROCOLEUS TENERRIMUS Gom.

D.—Holme to Blakeney. Z.—Marshes. O.—All the year. N.—Rare, mixed up with other species. Never abundant.

HYDROCOLEUM LYNGBYACEUM Kütz.

D.—Scolt. Z.—All marshes. O.—Late summer and autumn. N.—A rare species, sometimes occurring locally in quantity.

RIVULARIACEAE.**CALOTHRIX CONFERVICOLA** C. A. Agardh.

D.—Holme to Blakeney. Z.—All marshes. O.—All the year. N.—An infrequent species, epiphytic upon marsh algae or living in salt pans.

CALOTHRIX CONFERVICOLA C. A. Agardh var **PURPUREA** Born. & Flah.

D.—Cromer. Z.—Between tide-marks. N.—Very rare. Epiphytic. Recorded in Newton and recently found at Cromer on *Chaetomorpha melagonium*.

CALOTHRIX CONSOCIATA Born. & Flah.

D.—Scolt and Cley marshes. O.—All the year. N.—A very rare species, only recorded from Norfolk, where it is met infrequently. Grows epiphytically on the algae inhabiting the marshes. *Catenella repens* appears to be a common host. *Chaetomorpha* is cited by Newton as another host-plant.

CALOTHRIX SCOPULORUM C. A. Agardh.

D.—Marsh areas of Norfolk. Z.—Between the tide-marks, usually on high marshes. O.—All the year. N.—Forms brownish patches on the ground mixed up with *Rivularia*, *Phaeococcus*, and *Endoderma*.

CALOTHRIX PULVINATA C. A. Agardh.

D.—Holme to Blakeney. Z.—In the *Obionetum* and on *Suaeda* bushes on high marshes, also on the bare ground. O.—All the year. N.—Often occurs in dense masses covering the stems of *Suaeda fruticosa* and *Obione portulacoides* with a moss-like felt.

CALOTHRIX ENDOPHYTICA Cotton.

D.—Thornham to Blakeney. Z.—Upper marshes, wherever the host-plant occurs. O.—All the year. N.—Endophytic in *Enteromorpha torta*. Occurs sporadically. The infected filaments can be detected in the field, as they are a much darker green than usual. This is only the second record since the species was first discovered by Cotton (1912) at Clare Island. It is very difficult to remove the trichomes from the *Enteromorpha* tube, as they are fitted in very tightly.

RIVULARIA BIASOLETTIANA Menegh. : *Schizosiphon Warreniae* Casp.

D.—Scolt Head. Z.—Middle and upper marshes. O.—All the year. N.—A rare species. Distinguished in the field by the flattened nature of the cushion, which is a deep blue-black in colour.

RIVULARIA ATRA A. G. Roth (cf. Note 6 on p. 257)

D.—Thornham to Blakeney Z.—Upper marshes. O.—All the year.
N.—On firm soil on upper marshes.

RIVULARIA ATRA A. G. Roth var. **CONFLUENS** Farlow.

D.—Holme to Blakeney. Z.—Upper marshes and the edges of shingle ridges. O.—All the year. N.—The commonest form. Same as the typical species, except that the thallus is a confluent mass.

RIVULARIA NITIDA J. G. Agardh. Fig.: Fremy (1927), p. 192.

D.—Blakeney. Z.—Upper marshes. O.—All the year.

SCYTONEMATACEAE.**MICROCHAETE AERUGINEA** Batt. Fig.: Journ. Bot. 1892, p. 86.

D.—Blakeney. Z.—Sandy pools near high-water mark. O.—All the year.
N.—Epiphytic, usually on *Rhodochorton* spp. but other small algae may also be hosts.

TOLYPOTHRIX TENUIS Kütz. (cf. Note 4 on p. 256).

D.—Scolt Head Z.—Upper marshes. O.—All the year. N.—Very rare, only found once in the *Juncetum*.

NOSTOCACEAE.**NOSTOC COMMUNE** Vaucher.

D.—Scolt Head. Z.—Edge of old shingle laterals near high-water mark. O.—All the year. N.—Forms gelatinous flabby masses which lie loose on the ground. In the summer they tend to be overlooked as they shrivel up.

NOSTOC LINCKIA Born.

D.—Scolt Head. Z.—In the *Juncus* beds at extreme high-water mark. O.—All the year. N.—Not common, and the colonies are not macroscopic.

ANABAENA VARIABILIS Kütz.

D.—Scolt Head. Z.—In the *Juncus* beds at extreme high-water mark. N.—Very rare. Only found once.

ANABAENA TORULOSA Lagerh.

D.—Blakeney and Cley. Z.—Upper marshes. N.—Occurs as greenish black discoid or circular colonies on mud.

NODULARIA HARVEYANA Thur.

D.—Scolt Head. Z.—Upper marshes. O.—All the year. N.—A comparatively rare species, only occasional isolated threads being found. Lives on the mud mixed up with other Cyanophyceae.

CHLOROPHYCEAE.**ULOTRICHACEAE.**

ULOTHRIX FLACCA Thur. : *Lyngbya flacca* Harv.

D.—Whole coast. Z.—Between the tide-marks. O.—Annual, spring and summer. N.—A sporadic species, generally found in salt pans or pools. Recorded by Geldart as *Lyngbya flacca*.

ULOTHRIX SPECIOSA Kütz. : *Lyngbya speciosa* Carm.

D.—Thornham to Blakeney. Z.—Salt pans of middle marshes. O.—Spring. N.—Very abundant in spring forming a silky mat over the plants, or in salt pans or covering stones in the beds of small creeks.

ULOTHRIX PSEUDOFALCATA Wille.

D.—Blakeney. Z.—In the bed of the main channel on *Fucus vesiculosus*. O.—Spring

ULOTHRIX SUBFLACCIDA Wille (cf. Note 7 on p. 257).

D.—Wells. O.—Spring N.—A rare species, only found once, and then not in abundance.

CHAETOPHORACEAE.

PILINIA RIMOSA Kütz.

D.—Scole Head, Yarmouth. Z.—Middle and upper marshes. O.—All the year. N.—Common on *Obione* stems at the edges of creeks as a greenish crust. Probably occurs between Thornham and Blakeney.

ENDODERMA PERFORANS Huber (see Note 8, p. 257).

D.—Scole Head Island. Probably from Thornham to Blakeney. Z.—Middle marshes. O.—All the year, but most abundant in spring.

BLASTOPHYSA RHIZOPUS Reinke.

D.—Yarmouth. N.—Rare. Epiphytic on other algae.

ULVACEAE.

ENTEROMORPHA INTESTINALIS * Link f. **GENUINA** Hauck.

D.—Whole coast. Z.—Between tide-marks. O.—All the year. Most abundant in summer (see Note 9, p. 257).

ENTEROMORPHA INTESTINALIS Link f. **MAXIMA** J. G. Agardh.

D.—Thornham and Blakeney. Z.—Where fresh water runs into the sea. O.—All the year. N.—Only occurs in Blakeney main channel at the Cley end, and in Thornham main channel near the quay.

* Diagrams of the species of *Enteromorpha* can be found in Kützing's 'Tabulae Phycologicae', vi, 1856.

ENTEROMORPHA INTESTINALIS Link f. **FLAGELLIFORMIS** Le Jol.

D.—Thornham to Blakeney. Z.—On stones in the main channels. O.—All the year.

ENTEROMORPHA INTESTINALIS Link f. **MICROPHYLLA** Kjellm.

D.—Thornham to Blakeney. Z.—Low and middle marshes. O.—All the year. N.—A free-living species, occurring in isolated ribbons, but more commonly in a tangled mat. Not abundant.

ENTEROMORPHA INTESTINALIS Link f. **TUBULOSA** Kütz.

D.—Thornham to Blakeney. Z.—Low and middle marshes in the salt pans. O.—All the year. N.—Probably associated with stagnant water.

ENTEROMORPHA INTESTINALIS Link f. **CORNUCOPIAE** Kütz.

D.—Whole coast. Z.—On stones in the beds of channels. O.—All the year. N.—Distributed sporadically along the coast and is to be found in small streams where fresh water runs out into the sea.

ENTEROMORPHA INTESTINALIS Link f. **CRISPA** Agardh.

D.—Thornham to Blakeney. Z.—In dykes in enclosed marshes, or in creeks of very high marshes. O.—All the year. N.—This species is included as a marine form because it does appear in the creeks of salt marshes, especially where water is left in pools. It attains its best growth, however, in the ditches of the reclaimed marshes. This form presumably attains its best development in quiet waters which are fresh or brackish.

ENTEROMORPHA COMPRESSA Grev. f. **GENUINA** Grev.

D.—Whole coast. Z.—Between the tide-marks. O.—Spring, summer, and autumn. Rare in winter.

ENTEROMORPHA COMPRESSA Grev. f. **COMPLANATA** J. G. Agardh.

D.—Thornham to Blakeney. Z.—Protected sandy flats. O.—Spring to autumn. N.—Is confined on this coast to sandy or slightly muddy sand flats. The basal part of the thallus is always embedded showing that originally it had been attached to some substrate.

ENTEROMORPHA COMPRESSA Grev. f. **SUBSIMPLEX** J. G. Agardh.

D.—Thornham to Burnham Overy. Z.—High-water mark on stones and wooden piles. O.—Spring to autumn.

ENTEROMORPHA COMPRESSA Grev. f. **INTERMEDIA**, form. nov.

D.—Scole Head, Hunstanton. Probably more widely distributed. Z.—Main channel at Scole. Boulders near H.W.M., Hunstanton. N.—In the field may be confused with *E. intestinalis* f. *flagelliformis*, but differs from this in microscopic characters such as arrangement of cells and thickness of the membrane.

ENTEROMORPHA PROLIFERA J. G. Agardh f. **CAPILLARIS** Kütz (cf. note 10 on p. 258).

D.—Thornham to Blakeney, Hunstanton. Z.—On low sand or mud marshes or on mud banks in creeks. O.—All the year. N.—A very abundant species. Described by Carter from Canvey in the 'Journal of Ecology', 1933, where it is classed as *E. prolifera* form B II.

ENTEROMORPHA PROLIFERA J. G. Agardh f. **TRICHODES** Batt.

D.—Thornham to Blakeney. Z.—Beds of channels and low marshes. N.—Distinguished in the field from the previous form by its brighter green and the greater width of the parent thallus and also the extreme length of the branches. It is not a very common form.

ENTEROMORPHA PROLIFERA J. G. Agardh f. **TUBULOSA** Reinb.

D.—Holme to Blakeney. Z.—Middle marshes. O.—All the year. N.—A very common form, lying on the bare ground and also floating in salt pans. Recognized by its bright green colour and slimy feeling. The threads are generally unbranched, but occasionally they may be found with small spine-like branches.

ENTEROMORPHA PROCERA Ahln.

D.—Scolt Head. N.—A rare species only found on two occasions.

ENTEROMORPHA PROCERA Ahln. f. **DENUDATA** Ahln. Text-fig. 3, 1-3.

D.—Scolt Head. N.—Very rare. only found once and then it was washed up. Probably grows on the stones in the whelk-bed one mile off shore.

ENTEROMORPHA PROCERA Ahln. f. **MAXIMA**, form. nov.

D.—Blakeney. Z.—Main channel. N.—A very rare form. Occurs associated with *E. intestinalis* f. *maxima*, and, like it, probably thrives where there is a certain amount of fresh water admixed.

ENTEROMORPHA RAMULOSA Hook. f. **UNCINATA** Lyngb.

D.—Thornham to Blakeney. Z.—Salt pans and creeks of marshes. O.—All the year. N.—Not common.

ENTEROMORPHA RAMULOSA Hook. f. **ROBUSTA** Hauck.

D.—Thornham to Blakeney. Z.—In salt pans and on the edges of big creeks. O.—All the year.

ENTEROMORPHA RAMULOSA Hook. f. **TENUIS** Hauck.

D.—Scolt Head. Z.—In salt pans. N.—A rare form, only found occasionally.

ENTEROMORPHA MINIMA Naeg.

D.—Holme to Blakeney : Yarmouth to Sheringham. Z.—Edges of creeks, low marshes, on stones and Fucoids. O.—All the year, but most abundant in summer. N.—A common species found clothing the old stems of *Aster*

and *Obione* near the edges of large creeks. Sometimes it may be found on the plants of the open marsh, but usually it is associated with the creeks.

ENTEROMORPHA MICROCOCCA Kütz. f. **TORTUOSA** J. G. Agardh.

D.—Thornham to Blakeney. Cromer breakwaters. Z.—Low marshes near

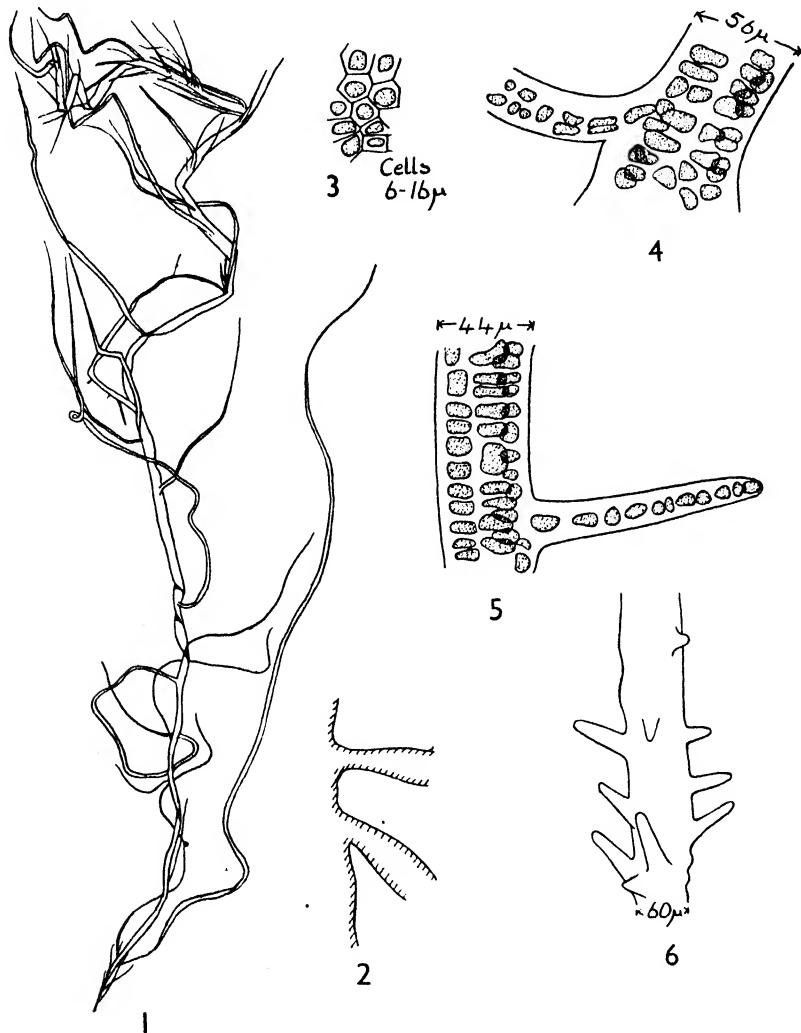


FIG. 3.—1-3, *Enteromorpha procera* var. *denudata*; 4-6, *Enteromorpha salina* var. *polycladoides*. 1, half nat. size.

the banks of large creeks. N.—Not very common at Scolt, but recorded as being frequent at Blakeney. It is not readily distinguished from the preceding species in the field. Abundant at Cromer.

ENTEROMORPHA TORTA Reinb.

D.—Holme to Blakeney. Z.—Between tide-marks. O.—All the year. N.—Very common, usually mixed up with threads of *Rhizoclonium implexum*. Forms 'ropes' on the sand flats. Covers the bare ground and also is abundant in salt pans.

ENTEROMORPHA RALFSII Harv.

D.—Thornham to Blakeney. Z.—Edges of creeks on lower marshes. N.—Not common. Forms thin threads which cling to the edges of the creeks of low marshes.

ENTEROMORPHA CLATHRATA J. G. Agardh.

D.—Whole coast. Z.—H.W.M. O.—All the year. N.—A fine thread-like species, not easily recognized in the field, where it resembles *E. torta*.

ENTEROMORPHA CLATHRATA J. G. Agardh f. **GRACILIS** Le Jol.

D.—Scolt Head. N.—A rare species, only found once.

ENTEROMORPHA CLATHRATA f. **LINKIANA** Batt.

D.—Scolt Head. N.—Rare. Probably grows also in deep water off the shore.

ENTEROMORPHA CLATHRATA J. G. Agardh f. **PROSTRATA** Le Jol.

D.—Thornham to Blakeney. Z.—Upper marshes. O.—All the year. N.—A common form on upper marshes, where it covers the bare ground. Is easily recognized in the field by the contorted thallus bearing numerous short spiny branches visible to the naked eye.

ENTEROMORPHA CHARTACEA Schiff.

D.—Sheringham to Cromer. Z.—H.W.O.N.T. N.—Common in this area. Originally thought to be a form of *E. clathrata* f. *Linkiana* cf. Note 9.

ENTEROMORPHA PARADOXA Kütz. f. **TENUISSIMA** Kütz. : *E. Hopkirkii* M'Calla.

D.—Scolt Head, Hunstanton. N.—Rare.

ENTEROMORPHA SALINA Kütz. var. **POLYCLADOS** Kütz.

D.—Scolt Head. Z.—Middle and upper marshes. O.—All the year. N.—Not common. Unrecognizable in the field. Grows on the ground mixed up in felts containing *E. torta* and *Rhizoclonium implexum*.

ENTEROMORPHA ERECTA Hook.

D.—Scolt Head. O.—Summer and autumn. N.—Frequent in the main creek of Missel Marsh.

ENTEROMORPHA CRINITA J. G. Agardh.

D.—Scolt Head. N.—A rare species, dredged in the bay and sometimes found washed up on the marshes.

MONOSTROMA WITTRICKII Born. Fig.: Hauck, Meeresalgen, 1885, p. 423.
 D.—Scolt Head. N.—A rare species found in salt pans (cf. Note 11, p. 259).

MONOSTROMA LATISSIMUM Wittr.

D.—Thornham, Wells, Stiffkey. Z.—Upper marshes. N.—In salt pans, floating.

MONOSTROMA LACERATUM Thur.

D.—Scolt Head. Probably Thornham to Blakeney. Z.—Middle and upper marshes. N.—Grows on the ground or in salt pans.

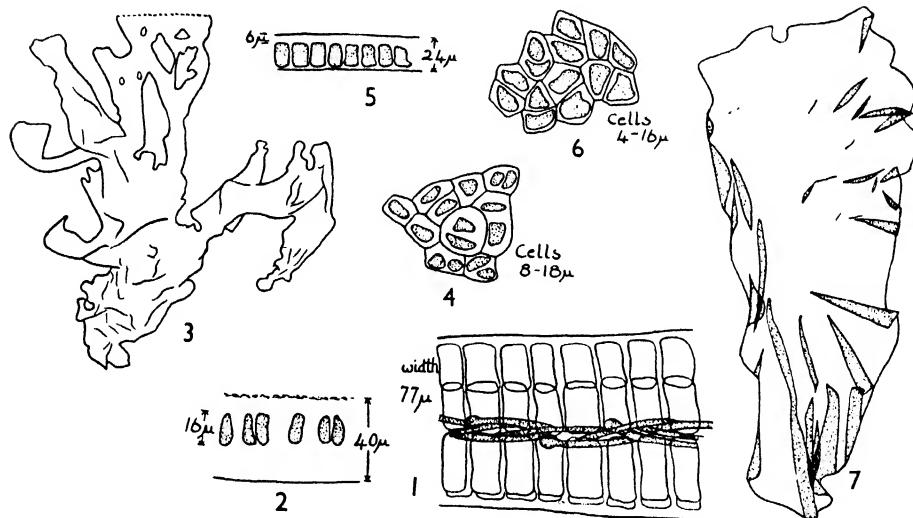


FIG. 4.—1, *Calothrix endophyticum* within *Enteromorpha torta*; 2-4, *Monostroma laceratum*; 5-7, *Monostroma latissimum*. 3, $\times \frac{1}{4}$, and 7, $\times \frac{9}{32}$.

MONOSTROMA ORBICULATUM Thur.

D.—Thornham to Blakeney. Z.—Middle and upper marshes. O.—Spring and summer. N.—A very abundant species, growing on the bare soil and in salt pans.

MONOSTROMA CREPIDINUM Farlow.

D.—Scolt Head. N.—An infrequent species growing in salt pans.

MONOSTROMA GREVILLEI Wittr. : *Ulva lactuca* Linn.

D.—Thornham to Blakeney. Z.—Mud flats of low marshes and sand pools. O.—Spring. N.—Easily recognized in the field by its delicate texture, bright green colour, and saccate shape, which is retained even in quite old plants.

PERCURSARIA PERCURSA Rosenv. : *Enteromorpha percursa* J. G. Agardh.
 D.—Whole coast. Z.—Upper half of tidal range. O.—All the year.

ULVA LACTUCA Linn. var. LATISSIMA DC. : *U. latissima* J. G. Agardh.
 D.—Whole coast. Z.—On stones on the foreshore or in the beds of channels.
 O.—All the year, but particularly abundant in summer.

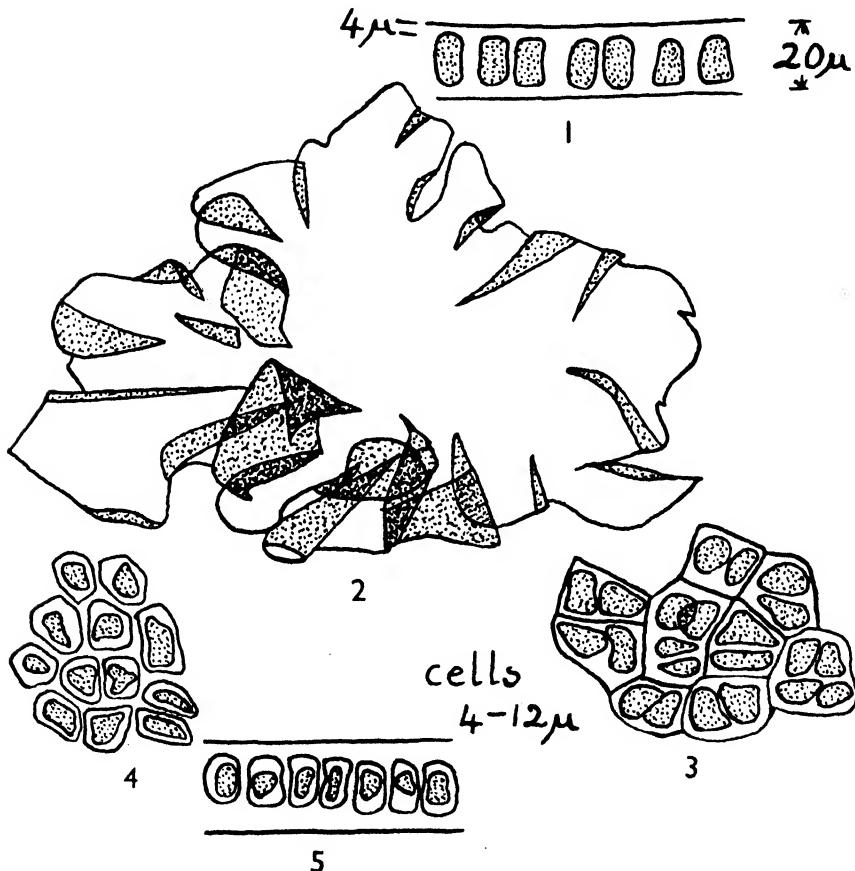


FIG. 5.—1-3, *Monostroma crepidinum*; 4 & 5, *M. orbiculatum*, after Wittrock.
 2, nat. size; the others, $\times 300$.

ULVA LINZA J. G. Agardh var. LANCEOLATA Kütz.
 D.—Whole coast. Z.—On stones near low-water mark.

SCHIZOGONIACEAE.

PRASIOLA STIPITA Suhr.
 D.—Yarmouth. N.—Recorded in Geldart's list, but no further data given.

CLADOPHORACEAE.

CLADOPHORA PELLUCIDA Kütz.

D.—Whole coast. Z.—Low-water mark or submerged off-shore. O.—All the year, most frequent in spring and summer.

CLADOPHORA NEESIORUM Kütz. var. HUMILIS Batt. : *C. humilis* Kütz.

D.—Scolt Head. Z.—On stones in the main channel. N.—A rare species only found once.

CLADOPHORA RUPESTRIS Kütz.

D.—Whole coast. Z.—Lower part of tidal area. O.—All the year. Most abundant in spring and summer.

CLADOPHORA UTRICULOSA Kütz. : *C. laetevirens* Harv.

D.—Thornham to Blakeney, Cromer, Runton, Sheringham. Z.—In sandy pools on the low marshes. L.W.O.N.T. O.—Spring and summer.

CLADOPHORA UTRICULOSA Kütz. var. DIFFUSA Hauck : *C. diffusa* Harv.

D.—Cromer. N.—Rare. Regarded as doubtful for this coast. Further records would be desirable.

CLADOPHORA GRACILIS Kütz.

D.—Cromer, Blakeney, Runton. O.—Annual. N.—Thrown up at Cromer. Grows on the beach at Runton.

CLADOPHORA SERICEA Kütz. : *C. crystallina* Kütz.

D.—Thornham to Blakeney, Hunstanton. Z.—Sandy pools and beds of creeks. O.—Spring and summer. N.—A very abundant species in the salt-marsh area. Common on boulders near H.W.M. at Hunstanton.

CLADOPHORA GLAUCESCENS Harv.

D.—Hunstanton, Runton. Z.—H.W.O.N.T. to M.T.

CLADOPHORA FLEXUOSA Harv.

D.—Whole coast. Z.—Pools and beds of channels. N.—Not very common.

CLADOPHORA REFRACTA Aresch.

D.—Cromer. No further data given in Geldart's list.

CLADOPHORA ALBIDA Kütz.

D.—Cromer. No further data given in Geldart's list.

CLADOPHORA EXPANSA Kütz.

D.—Thornham to Blakeney. Z.—Low muddy marshes and salt pans on higher marshes. O.—Spring and summer. N.—A fairly frequent species, occurring as a free-living form in salt pans and on marshes.

CLADOPHORA FRACTA Kütz. var. *MARINA* Hauck.

D.—Whole coast. Z.—Muddy marshes near L.W.M. O.—Spring and summer. N.—Another free-living form, attached only in the early stages of its existence. Is often found among mussels.

CLADOPHORA FRACTA Kütz. var. *FLAVESCENS* Batt. : *C. flavesiensis* Harv.

D.—Scolt Head, Cromer, Runton. N.—Not common.

CLADOPHORA FRACTA Kütz. var. *FLEXUOSA* Batt.

D.—Scolt Head. N.—Also recorded for Norfolk in Newton's 'Handbook' and in Geldart's list.

CLADOPHORA ARCTA Kütz.

D.—Cromer. No further data given in Geldart's list.

CLADOPHORA LANOSA Kütz.

D.—Cromer area. N.—Only recorded in the earliest list. Probably would be found again if searched for.

CHAETOMORPHA TORTUOSA Kütz. : *Conferva tortuosa* Dillw.

D.—Cromer area. O.—All the year. N.—Forms tangled mats around other algae, as this is one of the unattached forms.

CHAETOMORPHA LITOREA Cooke : *Conferva litorea* Harv.

D.—Wells marshes. Z.—H.W.O.S.T. O.—All the year. N.—A rare species, only one patch found, the filaments growing on the mud near a salt pan on a high marsh.

CHAETOMORPHA LINUM Kütz. : *Conferva sutoria* Berk.

D.—Whole coast. O.—Summer. N.—A rare species, occurring spasmodically.

CHAETOMORPHA AEREA Kütz. : *Conferva aerea* Dillw.

D.—Scolt Head, Salthouse, Hunstanton. Z.—Low marshes at Scolt, dykes at Salthouse. O.—All the year. N.—Locally abundant. Grows amongst the mussels at Hunstanton, in the Cockle Bight and Ternery mussel marsh at Scolt, and in the dykes at Salthouse.

CHAETOMORPHA MELAGONIUM Kütz. : *Conferva melagonium* Web. & Mohr.

D.—Scolt Head, Runton. Z.—Beds of main creek and upper parts of tidal area. O.—All the year. N.—Grows attached to stones amongst the mussel beds in Norton Creek at Scolt. In pools on the beach at Runton.

RHIZOCOLONIUM KOCHIANUM Kütz. var. *ARENICOLA* Newton : *Conferva arenicola* Berk.

D.—Thornham, Scolt Head. Z.—Upper marshes. O.—All the year. N.—Not a common species. Occurs mixed up with *R. implexum*, from which it can be distinguished by its smaller width and greater length of cell.

RHIZOCLONIUM IMPLEXUM Batt.

D.—Holme to Blakeney. Z.—Between the tide-marks. O.—All the year. N.—Very common. Occurs in mats lying on the bare ground or in salt pans. Rarely occurs pure, but is usually associated with *E. torta*. Characterized by the complete absence of rhizoidal branches.

RHIZOCLONIUM ARENOSUM Kütz. : *Conferva arenosa* Carm.

D.—Scolt Head. Z.—Upper marshes. N.—Rare. Only occurring sporadically and never in great abundance.

RHIZOCLONIUM RIPARIUM Harv.

D.—Scolt Head, Blakeney. Z.—H.W.O.N.T. O.—All the year. N.—Not common at Scolt, frequent at Blakeney.

UROSPORA ISOGONA Batt. : *Conferva Youngana* Dillw.

D.—Thornham, Scolt Head, Wells, Blakeney. Z.—H.W.O.S.T. to M.T. O.—Spring and summer. N.—Common in salt pans in spring and also mixed with *Ulothrix* on stones in the beds of small creeks.

GOMONTIACEAE.**GOMONTIA POLYRHIZA** Born. & Flah.

D.—Thornham to Blakeney, Cromer. Z.—On stones and shells on low marshes and on sand flats. O.—All the year. N.—A common species, covering shells and stones with a green crust. Found wherever there are shells washed up.

BRYOPSIDACEAE.**BRYOPSIS HYPNOIDES** Lamour.

D.—Scolt Head. Z.—Middle tide. N.—Rare. Only a few plants found, growing in a pool on a sand flat. These plants have been found for several successive years.

BRYOPSIS PLUMOSA C. A. Agardh.

D.—Runton, Cromer. Z.—M.T. N.—In cracks in the beach at Runton and in a large pool at Cromer.

VAUCHERIACEAE.**VAUCHERIA DICHOTOMA** Lyngb. var. **SUBMARINA** C. A. Agardh.

D.—Stiffkey, Burnham Deepdale. Z.—H.W.O.S.T. O.—All the year. N.—In salt pans on the marshes. The growth of the plants is luxuriant and they form a *Vaucheria* 'forest' in the pans.

VAUCHERIA THURETII Woron.

D.—Holme to Blakeney. Z.—M.T. O.—All the year. N.—The most frequent *Vaucheria*. Colonizes the mud banks of large creeks and also the mud flats. Recognized by its dark, almost blue-green, caespitose tufts. Acts as a very efficient mud-binder.

VAUCHERIA SYNANDRA Woron.

D.—Blakeney. O.—All the year. N.—Apparently rare. Confined to the upper marshes.

VAUCHERIA SPHAEROSPORA Nordst. var. **SYNOICA** Nordst. (cf. Note 13 on p. 259).

D.—Holme to Blakeney. Z.—Upper marshes. O.—All the year. N.—A common species, usually found on high marshes, especially under bushes of *Suaeda fruticosa*.

VAUCHERIA CORONATA Nordst.

D.—Scolt Head, Blakeney, Morston. Z.—H.W.S.T. O.—All the year. N.—Found associated with *Juncus maritimus*. Sexual reproduction abundant in spring.

PHAEOPHYCEAE.**ECTOCARPACEAE.****ECTOCARPUS CONFEROIDES** Le Jol.

D.—Whole coast. Z.—M.T. and below. O.—All the year, most frequent in spring and summer. N.—A common species, epiphytic on other algae or attached to stones or entangled among other algae on low mud flats.

ECTOCARPUS CONFEROIDES Le Jol. var. **SUBULATUS** Hauck : *E. amphibius* Harv.

D.—Thornham to Cley. Z.—Upper marshes. N.—Occurs in salt pans. Not infrequent.

ECTOCARPUS FASCICULATUS Harv.

D.—Scolt Head, Cromer. Z.—Norton Creek in running water. N.—Rare, only a few specimens found. Occasionally occurs epiphytically on *Laminaria saccharina* and the small size of these plants is apt to be misleading.

ECTOCARPUS TOMENTOSUS Lyngb.

D.—Cromer area. Z.—Same as host. N.—Epiphytic on *Fucus vesiculosus* and *Fucus serratus*.

ECTOCARPUS HINCKSIAE Harv.

D.—Blakeney Point. N.—Rare, epiphytic on *Laminaria saccharina*.

ECTOCARPUS GRANULOSUS C. A. Agardh.

D.—Cromer. No further data given in the earlier lists.

PYLAIELLA LITTORALIS Kjellm. : *Ectocarpus littoralis* Kütz. (cf. Note 14 on p. 259).

D.—Whole coast. Z.—Between the tide marks. O.—All the year. N.—Very common, growing epiphytically on other algae or on stones or mud.

ELACHISTACEAE.

LEPTONEMA FASCICULATUM Reinke var. **SUBCYLINDRICA** Rosenv.
 D.—Scolt Head. Z.—Same as host. N.—On *Laminaria saccharina* in Norton Creek.

ELACHISTEA FUCICOLA Fries.

D.—Whole coast. Z.—Same as host. O.—All the year. N.—Abundant on *Fucus vesiculosus* and its marsh forms, and *F. serratus*.

ELACHISTEA SCUTULATA Duby.

D.—Cromer area. Z.—Same as host. O.—Summer. N.—Epiphytic on *Himanthalia lorea*.

SPOROCHNACEAE.

SPOROCHNUS PEDUNCULATUS C. A. Agardh.
 D.—Runton. No further data given in the earlier lists.

MESOGLOIACEAE.

CHORDARIA FLAGELLIFORMIS C. A. Agardh.
 D.—Cromer. Probably near low-water mark. O.—Summer.
CASTAGNEA VIRESSENS Thur. : *Mesogloia virescens* Carm.
 D.—Cromer. O.—Summer. Z.—Pools in lower half of tidal zone.

MYRIONEMACEAE.

MYRIONEMA STRANGULANS Grev. var. **TYPICA** Batt.
 D.—Scolt Head, Blakeney, Cromer. Z.—Same as host. O.—Summer.
 N.—Grows epiphytically on *Ulva latissima*. Found once on *Phyllitis Fascia*.
RALFSIA CLAVATA Farlow : *Myrionema clavatum* Harv.
 D.—Thornham to Blakeney, Runton. Z.—M.T. O.—All the year. N.—Dark brown circular patches on stones in pools and in the channels.

DESMARESTIACEAE.

DESMARESTIA VIRIDIS Lamour.
 D.—Cromer area. Z.—L.W.O.S.T. O.—Summer.
DESMARESTIA ACULEATA Lamour.
 D.—Yarmouth. Probably a cast-up from a bed off-shore.
DESMARESTIA LIGULATA Lamour.
 D.—Cromer area. Probably a cast-up from the bed off-shore.

ARTHROCLADIA VILLOSA Duby.

D.—Scolt Head, Cromer area. Z.—Deep water. O.—Summer. N.—Is washed up occasionally on the beach and into Burnham Overy harbour during the summer months.

HYDROCLATHRACEAE.**COLPOMENIA SINUOSA** Derb. & Sol. : Oltmanns, Band II (1922), p. 64.

D.—Thornham. Z.—H.W.M.O.S.T. O.—All the year. N.—Grows in two salt pans only on a high marsh, but is very abundant.

ASPEROCOCCACEAE.**ASPEROCOCCUS FISTULOSUS** Hook. : *A. echinatus* Grev.

D.—Scolt Head, Morston, Cromer. Z.—H.W.O.N.T. O.—All the year, but most abundant in spring and early summer. N.—Grows on stones in pools and among mussels and *Zostera nana* on mud flats.

STRIARIA ATTENUATA Grev.

D.—Wells. Z.—High marsh. O.—Spring and summer. N.—Grows in salt pans on *Polysiphonia fibrata*.

MYRIOTRICHIA FILIFORMIS Harv.

D.—Cromer, Wells. O.—Summer. N.—Epiphytic on other algae. Also found on *Zostera nana* in a salt pan at Wells.

SCYTOSIPHONACEAE.**PHYLLOTIS ZOSTERIFOLIA** Reinke.

D.—Scolt Head. N.—Very rare, only found occasionally in tide-pools and stony creeks.

PHYLLOTIS FASCIA Kütz. (cf. Note 15 on p. 260).

D.—Scolt Head, Morston, Blakeney Point, Cromer. Z.—In the main channels. O.—All the year, most abundant in spring. N.—Common on stones in pools and in the beds of large channels.

SCYTOSIPHON LOMENTARIUS J. G. Agardh. : *Chorda lomentaria* Lyngb.

D.—Scolt Head. N.—Rare. Grows in pools with stony beds.

PUNCTARIACEAE.**PUNCTARIA PLANTAGINEA** Grev.

D.—Cromer area. O.—Spring and summer.

PUNCTARIA LATIFOLIA Grev.

D.—Blakeney. O.—Spring and summer. N.—Rare, only a few specimens found.



FIG. 6.—1, *Phyllitis zosterifolia*, $\times \frac{1}{2}$; 2, *Callithamnion tenuissimum*, $\times 50$
(after Kützing).

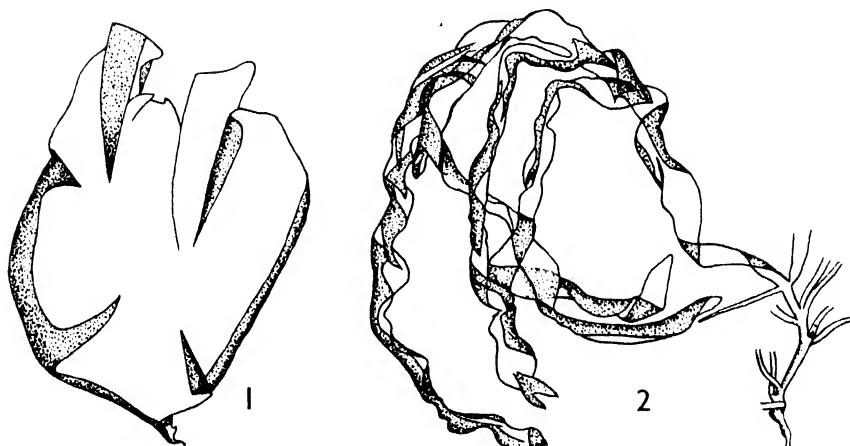


FIG. 7.—1, *Phyllitis Fascia*; 2, *Dumontia incrassata* var. *crispata*. Both $\times \frac{1}{2}$.

PHLOEOSPORA BRACHIATA Born. : *Ectocarpus brachiatus* Harv. (cf. Note 16 on p. 260).

D.—Cley. No further data available.

SPHACELARIACEAE.

SPHACELARIA RADICANS Harv.

D.—Thornham, Stiffkey. Z.—Upper marshes. O.—All the year. N.—In two salt pans from each locality. Abundant in these.

SPHACELARIA CIRRHOSA C. A. Agardh var. **PENNATA** Hauck.

D.—Cromer. Z.—L.W.O.S.T. O.—All the year.

SPHACELARIA CIRRHOSA C. A. Agardh var. **FUSCA** Holm. & Batt. : *S. fusca* Harv.

D.—Cley. N.—A rare species. Recorded in Batters' List.

CHAETOPTERIS PLUMOSA Kütz. : *Sphacelaria plumosa* Harv.

D.—Scolt Head. Z.—Deep water. N.—A deep-water form cast up fairly frequently in the summer.

CLADOSTEPHACEAE.

CLADOSTEPHUS SPONGIOSUS J. G. Agardh.

D.—Runton. Z.—L.W.M.O.S.T.

CLADOSTEPHUS VERTICILLATUS J. G. Agardh.

D.—Scolt Head, Cromer area. Z.—L.W.M. and below. O.—All the year. N.—Usually grows in deep water off-shore and is thrown up.

STYPOCAULACEAE.

STYPOCAULON SCOPARIUM Kütz. : *Sphacelaria scoparia* Lyngb.

D.—Cromer area. Z.—Deep water. N.—Probably cast up, but no data given.

CUTLERIACEAE.

CUTLERIA MULTIFIDA Grev.

D.—Cromer area. N.—Rare. Paget's list.

CHORDACEAE.

CHORDA FILUM Lamour.

D.—Scolt Head, Blakeney. Z.—In bed of harbours. O.—Summer. N.—Grows on the shingle bed of Blakeney harbour and of Norton Creek at Scolt.

LAMINARIACEAE.

LAMINARIA SACCHARINA Lamour.

D.—Whole coast. Z.—L.W.O.N.T. and lower. O.—All the year.
 N.—Common in the main channels at Scolt and Blakeney.

LAMINARIA SACCHARINA Lamour. var. PHYLLITIS Le Jol.: *L. Phyllitis* Lamour.

N.—Recorded by Paget and noted by him as rare. Locality not given.

ALARIA ESCULENTA Grev.

D.—Cromer. Z.—Always submerged. O.—All the year.

TILOPTERIDACEAE.

TILOPTERIS MERTENSII Kütz.: *Ectocarpus Mertensii* Harv.

D.—No data. N.—A deep-water species. Very rare, recorded by Paget.

ACINETOSPORA PUSILLA Born. var. CRINITA Batt.: *Ectocarpus crinitus* Carm.

D.—Thornham, Scolt, Blakeney, Runton. Z.—Low marshes. L.W.O.N.T. at Runton. O.—All the year. N.—Occurs lying on bare sand flats and more frequently in salt pans in the *Asteretum*. Forms a very efficient binder of sand on the chalk beach at Runton.

DICTYOTACEAE.

DICTYOTA DICHOTOMA Lamour.

D.—Scolt Head, Cromer area. Z.—Low-water mark. O.—Spring and summer. N.—At Scolt grows in Norton Creek among the mussel-beds.

TAONIA ATOMARIA J. G. Agardh.

D.—Cromer, Runton. Z.—L.W.O.S.T.

FUCACEAE.

FUCUS CERANOIDES Linn.

D.—Cromer area. O.—All the year. N.—Found once in 1806 and then sparingly (Paget's list). This may have been thrown up from some distance away and should be regarded as suspicious, requiring further records.

FUCUS SPIRALIS Linn. var. PLATYCARPUS Thur. Fig.: Oltmanns, II, 1922, p. 191.

D.—Scolt Head, Burnham Overy, Blakeney, Morston, Hunstanton, Cromer. Z.—H.W.O.N.T. O.—All the year. N.—The species and its variety are both common. Forms a zone below *Pelvetia* along Norton Creek at Scolt. Frequent on the Cromer breakwaters.

FUCUS VESICULOSUS Linn.

D.—Whole coast. Z.—M.T. and above. O.—All the year.

FUCUS VESICULOSUS Linn. var. **DIVARICATUS** Good. & Wood.

D.—Scolt Head, Blakeney. Z.—M.T. and above. O.—All the year. N.—Grows mixed with the type-species. Characterized by having few bladders and those present are always in the forks of the thallus.

FUCUS VESICULOSUS Linn. var. **SPHAEROCARPUS** J. G. Agardh.

D.—Scolt Head, Blakeney, Burnham Overy. Z.—Mud and shingle flats. O.—All the year. N.—Forms a zone rather higher than the two preceding species. Characterized by much branching at the apices and small swollen fruiting portions.

FUCUS VESICULOSUS Linn. var. **EVESICULOSUS** Cotton.

D.—Scolt Head, Blakeney, Morston, Hunstanton. Z.—Low mud flats. O.—All the year. N.—Grows amongst mussels on soft mud flats. Characterized by the absence of vesicles.

FUCUS VESICULOSUS Linn. megecad **LIMICOLA** ecad **VOLUBILIS** S. M. Baker (cf. Note 17 on p. 260). Fig.: Journ. Linn. Soc. Lond., Bot. XL, 1912, p. 285. D.—Thornham, Scolt Head, Blakeney, Wells, Stiffkey. Z.—Banks of large creeks. O.—All the year. N.—Rarely found with bladders at Scolt. Fruits regularly at Scolt, but rarely at Blakeney.

FUCUS VESICULOSUS Linn. megecad **LIMICOLA** ecad **CAESPITOSUS** S. M. Baker. Fig.: Journ. Linn. Soc. Lond., Bot. XLIII, 1915, p. 331.

D.—Thornham to Blakeney. Z.—Low marshes. O.—All the year. N.—A small form, embedded in mud amongst the *Salicornia*.

FUCUS VESICULOSUS Linn. megecad **LIMICOLA** ecad **MUSCOIDES** Cotton. Fig.: Clare Island Survey, 1912, part x, p. 127, pl. 6.

D.—Scolt Head, Brancaster Staithes. Z.—High marshes. O.—All the year. N.—Grows mixed up with plants of *Plantago maritima*. Occurs abundantly in isolated patches.

FUCUS SERRATUS Linn.

D.—Burnham Overy, Blakeney, Cromer area. Z.—M.T. and below. O.—All the year. N.—Grows on the breakwater at Burnham Overy and in the main channel at Blakeney.

ASCOPHYLLUM NODOSUM Le Jol. : *Fucus nodosus* Linn.

D.—Burnham Overy, Cromer area. Z.—Upper half of tidal zone. O.—All the year. N.—Isolated plants are found at Burnham Overy. Frequent at Cromer.

PELVETIA CANALICULATA Dene. & Thur. : *Fucus canaliculatus* Linn.

D.—Scolt Head, Blakeney Point. Z.—H.W.O.N.T. O.—All the year. N.—On rocky coasts this plant occupies a much higher position in relation

to the tidal levels. There is no firm substrate on this coast at these levels, and instead it is found growing attached to stones along the banks of the main channel.

PELVETIA CANALICULATA Dcne. & Thur. ecad **LIBERA** S. M. Baker. Fig.: Journ. Linn. Soc. Lond., Bot. XL, 1912, p. 278.

D.—Thornham to Blakeney. Z.—Low marshes. O.—All the year. N.—Grows as a free-living form lying amongst the phanerogams on the lower marshes. Reproduces by proliferations.

PELVETIA CANALICULATA Dcne. & Thur. ecad **CORALLOIDES** S. M. Baker. Fig.: Journ. Linn. Soc. Lond., Bot. XL, 1912, p. 281.

D.—Blakeney. Z.—Low marshes. O.—All the year. N.—See Note 18 on p. 261.

BIFURCARIA TUBERCULATA Stackh. : *Pycnophycus tuberculatus* Kütz.

D.—Cromer. No further data given in earlier lists.

HIMANTHALIA LOREA Lyngb.

D.—Cromer area. O.—All the year. Not common.

HALIDRYS SILIQUOSA Lyngb.

D.—Scolt Head, Runton. Z.—In shallow water offshore or in pools at L.W.M. O.—All the year. N.—Thrown up at Scolt.

CYSTOSEIRA ERICOIDES C. A. Agardh.

D.—Cromer area. No further data.

CYSTOSEIRA DISCORS C. A. Agardh.

D.—Yarmouth. N.—Washed up. The presence of this species requires confirmation. It may have been brought round by the currents from the S. coast.

CYSTOSEIRA FIBROSA C. A. Agardh.

D.—Cromer area. N.—Abundant in the winter of 1798 (Paget's list).

CRYPTOPHYCEAE.

PHAEOCOCCUS ADNATUS Näg. Fig.: Journ. Ecology, 1933, p. 202.

D.—Thornham to Blakeney. Z.—Upper marshes. O.—All the year. N.—Cf. Note 20 on p. 261.

RHODOPHYCEAE.

BANGIACEAE.

BANGIA FUSCO-PURPUREA Lyngb.

D.—Yarmouth. No further data in earlier lists.

BANGIA FUSCO-PURPUREA Lynbg. var. **CRISPA** Holm. & Batt.

D.—Norfolk. No other data given. N.—Recorded for Norfolk in Newton's 'Handbook'.

PORPHYRA UMBILICALIS J. G. Agardh var. **LACINIATA** J. G. Agardh.

D.—Whole coast. Z.—Upper tidal levels. O.—All the year.

PORPHYRA UMBILICALIS J. G. Agardh var. **VULGARIS** C. A. Agardh : *P. vulgaris* C. A. Agardh.

D.—Cromer area; Scolt Head, Blakeney, Hunstanton. O.—Spring and early summer. N.—Regarded by Knight (1931) as the winter form of var. *laciniata*.

ERYTHROTRICHEA CARNEA J. G. Agardh.

D.—Blakeney Point. N.—Epiphytic. No data as to host.

GONIOTRICHUM ELEGANS Le Jol. : *Bangia elegans* Chauv.

D.—Scolt Head. Z.—Same as host. N.—Epiphytic upon *Polysiphonia nigrescens*. Rare, only found once.

HELMINTHOCLADIACEAE.

ACROCHAETIUM ENDOZOICUM Hamel : *Chantransia endozoica* Darb.

D.—Scolt Head. Z.—Same as host. O.—All the year. N.—Grows parasitically, forming red spots in a sponge. The sponge is a deep-water form which is often washed up on the beach.

ACHROCHAETIUM VIRGATULUM J. G. Agardh. : *Callithamnion virgatum* Harv.

D.—Blakeney, in the main channel. N.—Epiphytic on various algae.

ACROCHAETIUM DAVIESII Naeg. : *Callithamnion Daviesii* Lyngb.

D.—Weybourne. N.—Recorded by H. D. Geldart.

ACROCHAETIUM SECUNDATUM Naeg. Fig. : Kütz. Tabulae Phycol. xi, pl. 18.

D.—Yarmouth. N.—Epiphytic on other algae, especially *Porphyra*.

CHAETANGIACEAE.

SCINAIA FURCELLATA Bivona : *Ginnania furcellata* Mont.

D.—Cromer. N.—Recorded as rare : Paget's list.

GELIDIACEAE.

GELIDIUM CORNEUM Lamour.

D.—No data. Probably Cromer area. Munford's list.

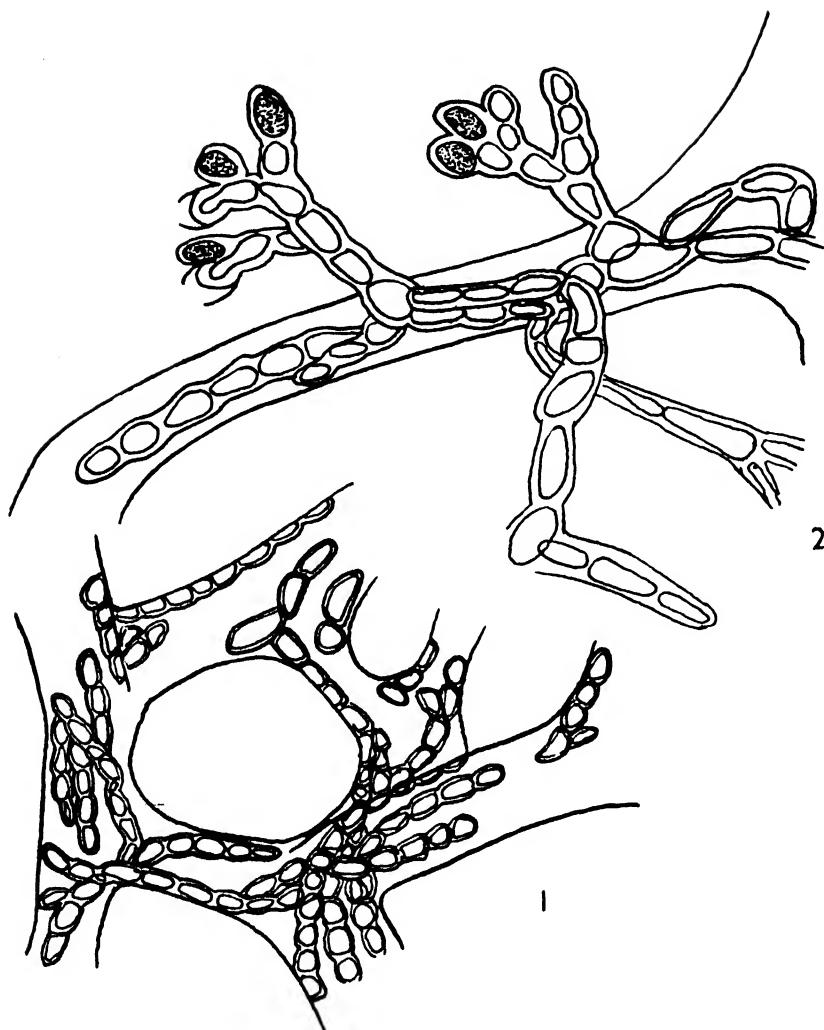
GELIDIUM CRINALE J. G. Agardh : *G. corneum* var. *crinale* auct.

D.—Runton. Munford's list. Z.—L.W.O.N.T., forming a turf.

WRANGELIACEAE.

NACCARIA WIGGHII Endl.

D.—Runton. L.W.M. and below. O.—Summer.

FIG. 8.—*Acrochaetium endozoicum*. Both figures $\times 200$, the second after Darbshire.

BONNEMAISONIA ASPARAGOIDES C. A. Agardh.

D.—No data. Probably Cromer area.

DUMONTIACEAE.

DUMONTIA INCRASSATA Lamour. : *D. filiformis* Grev.

D.—Cromer, Scolt Head. Z.—M.T. O.—Spring and summer. N.—Grows in Norton Creek and in Cockle Bight at Scolt.

DUMONTIA INCRASSATA Lamour. var. **CRISPATA** Batt.

D.—Scolt Head. Z.—M.T. O.—Spring and summer. N.—Grows in the stream in Norton Creek, and in the creek draining the Cockle Bight at the Ternery. Plants may grow to a considerable length.

DILSEA EDULIS Stackh. : *Iridea edulis* Harv.

D.—Norfolk. No data available.

NEMASTOMACEAE.

FURCELLARIA FASTIGIATA Lamour.

D.—Scolt Head, Cromer area. Z.—Shallow water off-shore. O.—All the year. N.—Thrown up frequently on the beach at Scolt and Cromer.

RHIZOPHYLLIDACEAE.

POLYOIDES ROTUNDUS Grev.

D.—Scolt Head, Runton, Sheringham. Z.—L.W.M.O.S.T. O.—All the year.

SQUAMARIACEAE.

CRUORIELLA DUBYI Schmitz : *Peysoniella Dubyi* Crouan.

D.—Scolt Head Z.—Shallow water off-shore. O.—All the year. N.—Dredged from the bay. Rare.

HILDENBRANDIA PROTOTYPUS Nardo.

D.—Scolt Head, Cromer to Sheringham. Z.—M.T. O.—All the year. N.—On stones in pools and in the beds of channels. Not a common species. The thallus is a brighter red than that of *Ralfsia clavata*.

CORALLINACEAE.

SCHMITZIELLA ENDOPHLOEA Born. & Batt.

D.—Scolt Head. Z.—Same as host. O.—Spring and summer. N.—In *Cladophora pellucida*.

MELOBESIA FARINOSA Lamour.

D.—Blakeney. Z.—Same as host. O.—All the year. N.—Epiphytic on *Cladophora rupestris*. Only one infected specimen was found, but further search might produce more.

LITHOTHAMNION LENORMANDII Foslie f. **TYPICA** Foslie.

D.—Scolt Head, Cromer to Sheringham. Z.—Shallow water of the sublittoral, and at L.W.M. O.—All the year. N.—On the flints in the bays. Dredged at Scolt.

CORALLINA OFFICINALIS Linn.

D.—Sheringham to E. Runton. Z.—L.W.M.N.T. O.—All the year.

CORALLINA RUBENS Ellis & Soland. : *Jania rubens* Lamour.

D.—Sheringham to Runton. Z.—L.W.M.O.S.T. O.—All the year.

DELESSARIACEAE.**DELESSARIA SANGUINEA** Lamour.

D.—Cromer area. Z.—Deep water off-shore. O.—All the year. Best in spring and summer.

MEMBRANOPTERA ALATA Kylin. : *Delessaria alata* Lamour.

D.—Cromer, Blakeney. Z.—Deep water off-shore. O.—All the year.

APOGLOSSUM RUSCIFOLIUM Kylin. : *Delessaria ruscifolia* Lamour.

D.—No data ; probably Cromer area.

HYPOGLOSSUM WOODWARDII Kylin. : *Delessaria hypoglossum* Lamour.

D.—Scolt Head, Cromer area. Z.—Deep water off-shore. O.—All the year, best plants found in summer. N.—Thrown up frequently on the beach at Scolt and also dredged in the bay.

NITOPHYLLUM PUNCTATUM Grev.

D.—Cromer, no further data given in earlier lists.

ACROSORIUM UNCIINATUM Kylin. : *Nitophyllum uncinatum* J. G. Agardh.

D.—Scolt Head, Blakeney, Cromer area. Z.—Sublittoral. O.—Spring and summer. N.—Dredged in bay at Scolt, also thrown up on beach, as also at Blakeney.

PHYCODRYS RUBENS Batt. : *Delessaria sinuosa* Lamour.

D.—Scolt Head, Cromer area. Z.—Shallow water off-shore. O.—All the year, best in summer. N.—Dredged in the bay at Scolt.

POLYNEURA GMELINI Kylin. : *Nitophyllum Gmelini* Grev.

D.—No data, probably Cromer area.

CRYPTOLEURA RAMOSUM Kylin. : *Nitophyllum laceratum* Grev.

D.—No data, probably Cromer area.

RHODOMELACEAE.

BOSTRYCHIA SCORPIOIDES Kütz.

D.—Holme to Blakeney. Z.—On all except the highest marshes. O.—All the year. N.—Very common, growing free-living on the marsh.

RHODOMELA SUBFUSCA C. A. Agardh.

D.—No data, probably Cromer area.

RHODOMELA LYCOPODIOIDES C. A. Agardh.

D.—Cromer.

LAURENCIA HYBRIDA Lenorm. : *L. caespitosa* Lamour.

D.—Scolt Head. Z.—M.T. N.—Rare, found on the shingle point opposite Beach Point and on the Ternery Mussel Marsh.

LAURENCIA PINNATIFIDA Lamour.

D.—Sheringham to E. Runton. Z.—L.W.M. N.—Abundant on the chalk at E. Runton.

HALOPITHYS INCURVUS Batt. : *Rytiphloea pinastroides* C. A. Agardh.

D.—Cromer. Z.—Deep water off-shore.

CHONDRIA DASYPHYLLA C. A. Agardh : *Laurencia dasypylla* Grev.

D.—Runton. Z.—L.W.O.N.T.

POLYSIPHONIA MACROCARPA Harv. : *P. pulvinata* Harv.

D.—Burnham Deepdale. N.—Grows on the sides of the sluice draining Deepdale marshes. Tetraspores in spring.

POLYSIPHONIA URCEOLATA Grev.

D.—Scolt Head, Blakeney, Cromer area. Z.—Lower part of tidal area. O.—Spring, summer, and autumn. N.—Grows in Norton Creek at Scolt and in the main channel at Blakeney.

POLYSIPHONIA NIGRA Batt. : *P. atro-rubescens* Grev.

D.—Blakeney. Z.—Main channel. N.—A rare species, only a few plants found.

POLYSIPHONIA FASTIGIATA Grev.

D.—Cromer area. Z.—Same as host, *Ascophyllum nodosum*. N.—Recorded in Munford's list.

POLYSIPHONIA FURCELLATA Hook.

D.—No data. Probably Cromer area.

POLYSIPHONIA ELONGATA Harv.

D.—Scolt Head, Blakeney, Cromer area. Z.—Main channels and L.W.M. O.—All the year. N.—Grows in main channel at Blakeney and in Norton Creek at Scolt.

POLYSIPHONIA FIBRATA Harv.

D.—Thornham, Wells, Stiffkey. Z.—High marshes. O.—All the year.
N.—Grows in a few salt pans in the three areas.

POLYSIPHONIA FIBRILLOSA Grev.

D.—Cromer.

POLYSIPHONIA VIOLENCEA Harv.

D.—Scolt Head, Burham Overy breakwater. Z.—Main channel. O.—All the year.

POLYSIPHONIA NIGRESCENS Grev.

D.—Scolt Head, Burnham Overy, Blakeney, Cromer area. Z.—M.T. and below. O.—All the year. N.—A common species in main channels growing on stones. The plants at Burnham Overy are exceptionally luxuriant.

PTEROSIPHONIA THUYOIDES Schmitz : *Rytiphloea thuyoides* Harv.

D.—Cromer to Sheringham. Z.—M.T. to L.W.O.S.T.

BRONGNIARTIELLA BYSSOIDES Bory : *Polysiphonia byssoides* Grev.

D.—Scolt Head, Cromer area. Z.—Sublittoral. O.—Summer. N.—Thrown up on the beach at Scolt in the summer fairly frequently.

HETEROSIPHONIA PLUMOSA Batt. : *Dasya coccinea* C. A. Agardh.

D.—Scolt Head, Blakeney, Cromer area. Z.—Sublittoral. O.—All the year, basal parts only in winter. N.—Thrown up frequently at Scolt and Blakeney.

CERAMIACEAE.**SPERMOTHAMNION TURNERI** Aresch. : *Callithamnion Turneri* C. A. Agardh.

D.—Cromer. N.—Found in June 1880 (H. D. Geldart).

PTILOTHAMNION PLUMA Thur.

D.—Cromer. N.—An epiphytic species on *Laminaria* stipes.

GRIFFITHSIA FLOSCULOSA Batt. : *G. setacea* C. A. Agardh.

D.—Whole coast. Z.—Sublittoral and main channels. O.—Spring and summer. N.—Very abundant off-shore at Scolt in the bay.

HALURUS EQUISETIFOLIUS Kütz. : *Griffithsia equisetifolia* C. A. Agardh.

D.—W. Runton. Z.—Deep water off-shore. L.W.S.T.

HALURUS EQUISETIFOLIUS Kütz. var. **SIMPLICIFILUM** J. G. Agardh : *Griffithsia simplicifilum* C. A. Agardh.

D.—Cromer area. N.—Recorded for Norfolk in Harvey's Phycol. Brit. Thrown up at Cromer July 1935.

PLEONOSPORIUM BORRERI Naeg. : *Callithamnion Borreri* Harv.

D.—Cromer. N.—Very rare, recorded in Paget's list.

PLEONOSPORIUM BORRERI Naeg. var. FASCICULATUM Helm. & Batt.: *Callithamnion fasciculatum* Harv.

D.—Yarmouth. N.—Very rare, further confirmation required.

RHODOCHORTON MEMBRANACEUM Magn.

D.—Scole Head, Brancaster. Z.—Same as host. O.—All the year. N.—Epizoic on and in the tubes of *Sertularia*; washed up from Brancaster Bay.

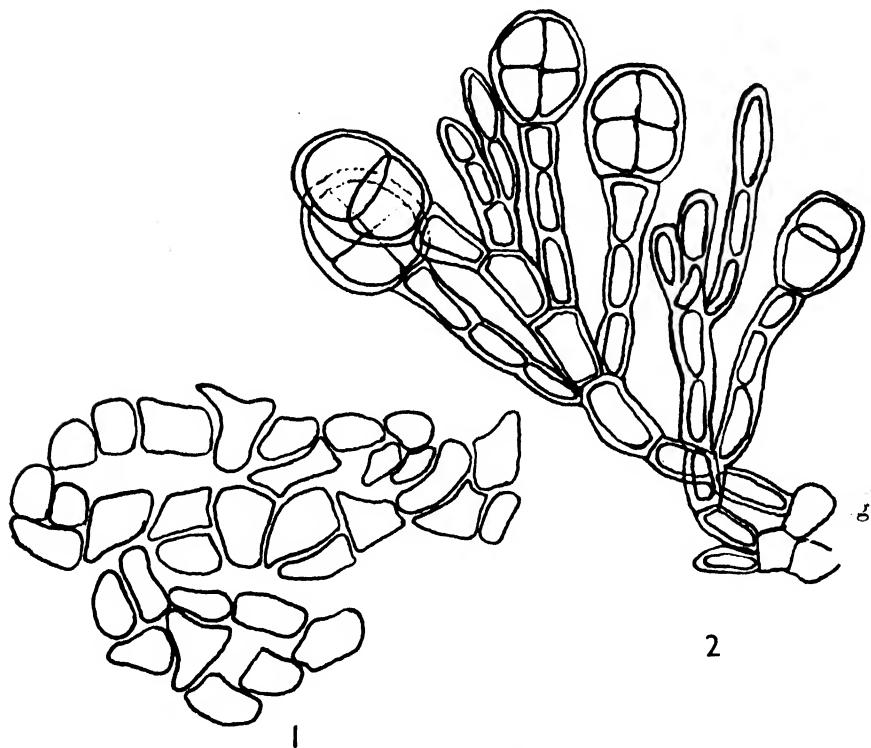


FIG. 9.—*Rhodochorton membranaceum*, $\times 200$.

RHODOCHORTON FLORIDULUM Näg.

D.—Thornham, Brancaster, Scole, Cromer area. Z.—Inter-tidal. O.—All the year. N.—On peat-beds and rocks on the foreshore.

RHODOCHORTON ROTHII Naeg.: *Callithamnion Rothii* Lyngb.
D.—Burnham Overy, Cromer, Burnham Deepdale. Z.—H.W.S.T. O.—All the year. N.—On Deepdale marsh sluice, on Burnham breakwater, on Cromer breakwaters.

CALLITHAMNION TENUISSIMUM Kütz.

D.—Scole Head. N.—A rare species, only a few plants found.

CALLITHAMNION BYSSOIDES Arn.

D.—Scolt Head, Blakeney, Runton, Cromer, Hunstanton. Z.—In beds of main channels. O.—Spring and summer. N.—Often epiphytic on *Chorda Filum*.

CALLITHAMNION POLYSPERMUM C. A. Agardh. Fig. : Knight & Parke (1931), pl. xvii.

D.—Scolt Head, Cromer, Hunstanton. Z.—Lower part of tidal area. O.—All the year. N.—Grows in Norton Creek at Scolt, where it is not an infrequent species.

CALLITHAMNION ROSEUM Harv.

D.—Whole coast. Z.—L.W.M. O.—Spring and summer. N.—Epiphytic on various algae ; grows in the beds of main channels along the marsh coast.

CALLITHAMNION HOOKERI C. A. Agardh. Fig. : Knight & Parke (1931), pl. xviii.

D.—Wells, probably also Cromer area. Z.—Main channels. N.—Cf. Note 22 on p. 261).

COMPSOTHAMNION THUYOIDES Schmitz : *Callithamnion thuyoides* C. A. Agardh.

D.—Cromer. N.—Recorded by Paget ; very rare.

PLUMARIA ELEGANS Schmitz : *Ptilota sericea* Harv.

D.—Cromer. Z.—Sublittoral. N.—Thrown up. Recorded in the old lists as *Ptilota plumosa*. Newton points out that this species is confined to N. England, and the plants must have been those of *P. elegans*.

ANTITHAMNION PLUMULA Thur. : *Callithamnion plumula* Lyngb.

D.—No data, probably Cromer area. Z.—Sublittoral.

CERAMIUM GRACILLIMUM Harv.

D.—Cromer. Z.—Deep water. O.—Summer. N.—Recorded by H. D. Geldart.

CERAMIUM TENUISSIMUM J. G. Agardh : *C. nodosum* Harv.

D.—Scolt Head, Cromer. Z.—Norton Creek. N.—A rare species, only found once, at Scolt ; recorded twice from Cromer.

CERAMIUM DIAPHANUM Roth.

D.—Cromer, Runton. O.—Summer. N.—Rare.

CERAMIUM DESLONGCHAMPSII Chauv.

D.—Scolt Head. Z.—Shallow water in the Bay. N.—A rare species, only found once ; requires further search and dredging.

CERAMIUM ARBORESCENS J. G. Agardh.

D.—Scolt Head, Stiffkey, Hunstanton. Z.—Main channel and pools. N.—Not infrequent; differs from *C. rubrum* in being slightly lighter in colour, not so robust, and cortication not so complete.

CERAMIUM RUBRUM C. A. Agardh var. **PEDICELLATUM** J. G. Agardh.

D.—Whole coast. Z.—M.T. downwards. O.—All the year.

CERAMIUM RUBRUM C. A. Agardh var. **CORYMBIFERUM** J. G. Agardh.

D.—Scolt Head. Z.—M.T. downwards. O.—All the year. N.—Probably has a wider distribution along the coast; occurs mixed with the other variety, but is not so common.

CERAMIUM ECHIONOTUM J. G. Agardh.

D.—Cromer to Sheringham. Z.—M.T. N.—In rock-pools, occasionally epiphytic.

CERAMIUM FLABELLIGERUM J. G. Agardh.

D.—Yarmouth, Hunstanton. Z.—H.W.O.N.T. N.—Epiphytic on other algae. Grows on the boulders at Hunstanton.

CERAMIUM ACANTHONOTUM Carm.

D.—Norfolk, Batter's List.

GIGARTINACEAE.**CHONDRUS CRISPUS** Lyngb.

D.—Scolt Head, also Cromer area. O.—All the year. N.—Washed up on the beach at Scolt; occurs sparingly at L.W.M. between Sheringham and Cromer.

PHYLLOPHORA EPIPHYLLA Batt. : *P. rubens* Grev.

D.—No data given in earlier lists.

PHYLLOPHORA MEMBRANIFOLIA J. G. Agardh.

D.—Scolt Head, Cromer area. Z.—Sublittoral at Scolt. L.W.S.T. at Cromer. O.—All the year. N.—A rare species at Scolt, where plants are occasionally washed up; probably grows in the bay.

AHNFELTIA PLICATA Fries.

D.—Scolt Head, Cromer area. Z.—Sublittoral. O.—All the year, not common.

CALLOPHYLLIS LACINIATA Kütz. : *Rhodymenia laciniata* Grev.

D.—No data, probably Cromer area. Z.—Sublittoral.

RHODOPHYLLIDACEAE.

CYSTOCLONIUM PURPUREUM Kütz. : *Hypnea purpurascens* Harv.

D.—Runton. Z.—M.T. downwards. N.—Grows on the chalk beach.

CATENELLA REPENS Batt. : *C. opuntia* Grev.

D.—Thornham to Cley. Z.—Middle and upper marshes. O.—All the year. N.—Cf. Note 23 on p. 261.

RHODOPHYLLIS BIFIDA Kütz. : *Rhodymenia bifida* Grev.

D.—No data given, probably Cromer area.

SPHAEROCOCCACEAE.

GRACILARIA CONFEROVIDES Grev.

D.—Scolt Head, Blakeney, Runton, Cromer. Z.—M.T. and main channels. O.—All the year. N.—Grows in main channels at Scolt and Blakeney, in cracks in the chalk beach at Runton.

CALLIBLEPHARIS CILIATA Kütz. : *Rhodymenia ciliata* Grev.

D.—Cromer, thrown up. Z.—Sublittoral.

CALLIBLEPHARIS LANCEOLATA Batt. : *Rhodymenia jubata* Grev.

D.—Yarmouth. N.—No data given in earlier lists.

RHODYMENIACEAE.

RHODYMENIA PALMETTA Grev.

D.—No data given. Geldart's list.

RHODYMENIA PALMATA Grev. var. **TYPICA** Batt.

D.—No data. Munford's list.

LOMENTARIA ARTICULATA Lyngb. : *Chylocladia articulata* Grev.

D.—No data given, probably Cromer area.

LOMENTARIA CLAVELLOSA Gaill. : *Chrysimenia clavellosa* Harv.

D.—Wells. Probably also Cromer area. N.—Only one plant found at Wells. No data about other locality.

CHYLOCLADIA KALIFORMIS Hook.

D.—No data given. Munford's list.

CHYLOCLADIA OVATA Batt. : *C. ovalis* Hook.

D.—No data given, probably Cromer area.

PLOCAMIUM COCCINEUM Lyngb.

D.—Whole coast. Z.—Sublittoral. O.—All the year. N.—Found as a cast up in considerable quantity in summer and autumn.

It will be noticed that many species have not been recorded since the earlier lists, and it is highly essential that these records be confirmed. I am informed by Mr. Cotton that the old record for *Callithamnion tetricum* must be erroneous and probably also that of *Halarachnion ligulatum*, and so these species have been omitted.

CRITICAL NOTES.

Note 1.—*Chroococcus turgidus* var. *maximus* (p. 222).

When these plants were first found they were thought to be the typical species. When, however, colonies were measured it was at once evident that they were far too big, and that they agreed better with var. *maximus*. The typical species has been recorded from Blakeney, but from what is known of these marshes it is almost certainly var. *maximus*. This form becomes abundant in the autumn months when it is mixed up with species of *Lyngbya* either on the bare soil, or more frequently in salt-pans.

Note 2.—*Oscillatoria brevis* var. *neapolitana* (p. 224).

This is a new record for a salt-marsh area but the plants found agree closely with the descriptions given. It has been recorded previously for salt and brackish water in Europe and North America. There appears to be very little difference between the variety and typical species.

Note 3.—*Oscillatoria acuminata* (p. 224).

This species has not previously been described from salt waters in Europe, but the specimens agreed well with the description given in Rabenhorst. It has been recorded previously from cold and warm waters of Europe, Ceylon, and Africa, but a form with short cells has been recorded by Setchell and Gardner from brackish water on the Californian coast. The diagram given here shews that the English form has shorter cells than the typical species, and must therefore be very similar to the Californian form.

Note 4.—*Tolypothrix tenuis* (p. 227).

This alga was only found once and there was some difficulty in determining it. There seems to be no doubt, however, that it represents this species. It has been recorded also for the Canvey salt-marshes by Carter (1933).

Note 5.—*Lyngbya aestuarii* var. *spectabilis* (p. 225).

A characteristic of this variety is said to be the change of colour in the sheath, namely hyaline in the outer layers and yellow in the inner. Many of the threads found at Scolt showed this feature, as is evident in fig. 2. At the same time, however, threads were found in which considerable changes took place in the sheath of the same filament in passing along it. These changes

lead one to suspect the validity of this variety—or, at any rate, the validity of using colour-variations in the sheath as a means of distinguishing different varieties of *Lyngbya aestuarii*. From fig. 2, 1-4, it will be seen that various depths of coloration may occur in the sheath, and drawings *a* and *b* illustrate two different effects seen on the same filament.

Note 6.—*Rivularia atra* (p. 227).

This is one of the commonest algae on the marsh mud, but it is rarely found in the typical form. Usually it is present in confluent masses which must be regarded as var. *confluens*. It forms a definite community and the other algae associated with it are *Phaeococcus adnatus* and *Endoderma perforans*. In other salt-marsh areas, especially the west coast of Ireland, the species is found on the vertical banks of creeks. Such a habitat is rare for this species along the Norfolk Coast. It has, however, been found colonizing such banks at Burnham Deepdale and Wells. The great abundance of this species on the creek banks of Irish marshes may be related to the difference in substrate. In Ireland the banks are built of peat which will withstand considerable wave action, whereas the Norfolk banks are of mud and are fairly readily eroded. In such a case erosion prevents the existence of the alga which probably would otherwise grow.

Note 7.—*Ulothrix subflaccida* Wille (p. 228).

Described as *U. implexa* Kütz. in Newton, Carter (1933) points out that Kützing did not intend to give this name to a marine species. Wille redescribed the marine forms and it should now be known under the name given above.

Note 8.—*Endoderma perforans* (p. 228).

This species has been recently described fairly fully by Carter (1933). She found that it occurred generally in colonies of *Rivularia atra*, but occasionally also grew on the bare soil. In Norfolk it appears to thrive better on the bare soil and not so well in the *Rivularia* colonies. No elongated threads, such as those figured by Carter, have been seen, but numerous short-branched threads are extremely common. The species is most abundant in the spring.

Note 9.—*Enteromorpha* (p. 228).

This is a notoriously difficult genus. On a rocky coast the forms are puzzling enough, but on salt-marshes the forms of the various species appear to attain their greatest range and variation. It was evident at the commencement of this work that the systematics of the genus would have to be worked out, and at present a revision of the genus is being undertaken. This revision is not yet complete and it is not proposed to give elaborate details here. The system used by most workers has been adhered to in this paper. Two new forms are described briefly for the first time, and a fuller description will appear in the revision.

E. compressa f. *intermedia*.

The plants are dark green in colour and are much branched at the base. They combine the characters of *E. prolifera*, *E. compressa*, and *E. ramulosa*. The cells are in rows in the branches but not in the main thallus : the membrane is often thickened on the inside. The branches are rarely constricted at the base (a character of *E. compressa*), whilst they may be widened and compressed at the apices.

E. procera (Ahln.) is a confusing species, because it bears considerable resemblance to some of the forms of *E. prolifera*. A rather attenuated form of *E. procera* has been found on a few occasions, whilst a very large form (which it is proposed to call f. *maxima*) has been collected at Blakeney. The plant of *E. procera* f. *denudata* is quite typical and agrees with Exsiccatae in Herbaria.

Another interesting record is that of *E. salina* f. *polyclados*. It is very distinctive and cannot be mistaken for any other species. Its identification was handicapped at first by the fact that it has not previously been recorded from Great Britain. In preparing the revision of the genus specimens of *E. salina* were examined, and it was then at once realized that this peculiar form from Scolt belonged to this species.

E. chartacea is another species new to Britain. It probably is common, but has been classified under other names, either as a form of *E. compressa* or of *E. clathrata*. See Schiffner's original description (Hedwigia, 1931).

Note 10.—*Enteromorpha prolifera* (p. 230).

This is perhaps the most puzzling of all the species. An attempt was made by Carter (1933) to clarify the position, and this work has been of great value in the further elucidation of the various forms. As Carter pointed out, the forms can be divided into those that proliferate freely and those that are simple or may have occasional short branches. The second group comprises the single form *tubulosa* and is very easy to recognize. The only species it could be confused with is *E. torta*, but the latter is solid or only slightly tubular, whereas f. *tubulosa* is markedly tubular. The arrangement of the cells in rows is also very obvious, the only disarrangement being at the points of emergence of the very rare branches. The other group contains four forms, possibly five, only three of which are recognised at Scolt. Forma *capillaris* is the form called B II by Carter, the name having been derived from a description by Kützing. It is very characteristic species forming long coarse hair-like ropes and strands of a grey-green colour. The proliferations are visible easily to the naked eye. It is also characterized by its habitat, which is upon soft sand or soft muddy sand on low marshes or in main channels. Form *trichodes* (B III of Carter) is rarer and grows in the large creeks of upper marshes, where it does not appear to be attached. It is sometimes found floating in the water of main channels. It is bright green in colour and is distinguished from the preceding form by the long branches (almost simple) and the wide main thallus.

Note 11.—*Monostroma* (p. 233).

A number of species of *Monostroma* have been recorded from this coast. Some of the determinations have very kindly been checked by Miss C. Dickinson at Kew. The species are not rare along this coast-line and occur in profusion, especially in spring and summer, lying on the bare marsh mud or occupying salt-pans. *M. laceratum* is relatively rare and is usually found growing on the bare mud of upper marshes. *M. orbiculatum*, *M. Wittrockii*, and *M. crepidinum* are more often to be found in salt-pans, but the first of these three species also occurs on the bare mud. *M. Grevillei* is a vernal species and grows on stones in pools or on shells partly buried in low mud-flats. It is the only species recognizable in the field, because it retains its saccate shape for a long period, and also it is bright green in colour, whereas the others, because of their gelatinous nature, tend to be a paler green.

Note 12.—*Urospora collabens* (p. 221).

This was recorded once only and under the name of *Conferra collabens*, and on that occasion it was on floating wood. This wood may have drifted from anywhere, and Geldart (1882) in his list doubts the advisability of retaining the species for Norfolk. In the present list, therefore, it has been omitted.

Note 13.—*Vaucheria sphaerospora* (p. 238).

In the 'Süsswasserflora Deutschlands' (1921) an unusual form of antheridium is described for this species. This type of antheridium was found on a specimen from Blakeney, in addition to the more usual antheridia. So far as the species of *Vaucheria* are concerned, it has been interesting to note that the plants from Blakeney bear the reproductive stages much more abundantly than do those from Scolt. The reason for this has not yet been ascertained.

Note 14.—*Pylaiella littoralis* (p. 238).

Three varieties of this species are described in Newton's 'Handbook' (1931), but from Knight's (1923) work on the species it would appear that the range of variation shown by the plant under different conditions would be sufficient to cover the recorded varieties. Although, therefore, plants corresponding to varieties *firma*, *opposita*, and *brachiata* have been found on this coast-line, in the List they are all regarded collectively as one species. Another interesting feature about *Pylaiella* is its habitat. From most areas it is recorded as an epiphyte on *Fucus vesiculosus*, *F. serratus*, and *Ascophyllum nodosum*. On the marshy coast of Norfolk the plants grow attached to stones or mud, and they rarely occur as epiphytes. One of the most striking cases is that of the escarpment of the Great Aster Marsh on Scolt Head Island, where numerous plants have been found growing attached to the mud. An elaborate life-cycle has been worked out by Knight (1923) with respect to the host-plants; but it is clear that so far as this area is concerned such a life-cycle in relation to host-plants may not exist.

Note 15.—*Phyllitis Fascia* (p. 240).

This species is extremely common along the marsh-coast, and is of interest because of the intense range of variation in the thallus that it exhibits. An extreme is depicted in fig. 7. At first these plants were thought to be distinct species or at least separate varieties, but careful examination has shown that they are nothing but ecological forms. The small form grows on mud and is only covered by the tide twice daily. The elongated forms grow in main channels and creeks where there is a strong current of water all the time, and the current, together with aeration and supply of salts, is probably responsible for the elongation. The rounded form was obtained from a beach pool where there is plenty of water, but the pool was at such a height that flooding only occurred with the higher tides. The rounded shape of the thallus may be a result of the comparatively stagnant nature of the water.

Note 16.—*Phloespora brachiata* (p. 242).

Recorded as rare from the Cley marshes in 1808 by Sir W. J. Hooker. Geldart (1882) was doubtful as to whether it should be included in the Norfolk list. It has been retained in the present list, but should be searched for again.

Note 17.—Marsh Fucoids (p. 244).

The marsh fucoids are probably the most interesting of all the Norfolk algae, and in some respects compensate for the general lack of species. Three marsh forms of *Fucus vesiculosus* have been recorded for this area, two described previously by Miss S. M. Baker (1912, 1915) from Blakeney and an additional one. The first of these is the form known briefly as *Fucus volubilis*. This is the largest, and is characterized by its free-living habitat and spirality of the thallus. For an account of the influence of the environment on these forms Baker's original paper should be consulted. Occasionally the plants bear vesicles similar to those of the normal species. These are said to be fairly frequent at Blakeney, but they are rare at Scolt. Reproductive conceptacles are likewise rare, and the plants propagate mainly by proliferations. In one locality on Scolt Head Island, however, the plants fruit regularly every year; the conceptacles and swollen thalli being similar to those of the normal plant. This form occurs along the banks of main creeks. *F. caespitosus* is a smaller form, also exhibiting some spirality, but it occurs embedded among plants of *Salicornia herbacea* on low marshes. It probably undergoes rather more exposure than the previous form. The smallest of the Fucoids is *Fucus muscoides* which is here recorded from Norfolk for the first time and constitutes the first record for the East Coast of England. The plants are fairly characteristic, and occur embedded in the ground on high marsh, especially where *Plantago maritima* is frequent. At present it has only been recorded for Norfolk from Scolt Head Island and Brancaster Staithes, but its small size may have resulted in plants being overlooked on other marsh areas.

The other Fucoid of interest is *Pelvetia canaliculata* form *libera*. This is

characterized by a curled and twisted thallus and its free-living habit. Reproductive conceptacles are very rare and the present author has never seen them. It reproduces normally by means of proliferations. It appears to grow at its best along this stretch of the Norfolk coast where it covers many acres of ground.

Note 18.—*Pelvetia canaliculata* var. *coralloides* (p. 245).

This is another of the marsh fucoids which has been recorded by Baker (1912, 1915) from the *Salicornia* marsh at Blakeney. The present author has searched for it on that marsh on several occasions but without success. The diagrams provided by Baker suggest that it may be only the proliferating portions of *f. libera*, and on the marshes at Blakeney examples of these proliferations have been found (with the parent thallus gone or nearly decayed) which show considerable resemblance to the plants described by Baker. It is evident that a re-investigation of this form would be desirable.

Note 19.—*Cystoseira barbata* and *C. granulata* (p. 221).

Both these species are recorded in Geldart's list (1882), but he doubts their authenticity, and so they have been omitted from the present list.

Note 20.—*Phaeococcus adnatus* (p. 245).

The true systematic position of this alga is uncertain, as its life-history has not yet been worked out. It was known previously as *Gloeocystis adnata* Nág., but it may really belong to the genus *Apistonema*.

Note 21.—*Callithamnion pedicellatum* (p. 221).

This species is recorded in Geldart's (1882) list from a live mussel-shell at Yarmouth, the mussel-shell being said to come from Blakeney. With this single record and the uncertainty of the source of the shell it has been thought advisable to omit the species from the present list.

Note 22.—*Callithamnion Hookeri* and *C. polyspermum* (p. 253).

Knight (1931) has pointed out that there are numerous intergrades between these two species, which make it doubtful whether they are two separate species. These intergrades occur on the Norfolk coast, and it is often very difficult to decide whether a plant belongs to *C. Hookeri* or *C. polyspermum*.

Note 23.—*Catenella repens* (p. 255).

A common species on the marsh part of the coast, where it grows in two different habitats and appears as two different forms. In the one case it grows as an epiphyte on the stems of *Obione portulacoides*. Under the conditions that exist here the plants appear as a rank form, the internodes long, and they are a dark purplish red in colour. In the other case it grows as a turf underneath bushes of *Suaeda fruticosa*, or out on the open marsh (the *Plantageto*), or epiphytically upon the stems of *Armeria*, *Plantago*, and

Spergularia in the *Plantageto*. Under these conditions the plants are dwarfed, the internodes are short, and they are a greenish purple in colour. The great difference in colour Rees (1935) has recently suggested may be due to the differences in light supply. Under the *Obione* bushes the amount of light presumably is poor and the red pigment is correspondingly highly developed, whereas in the other habitat the light supply is good and the red pigment is less conspicuous.

Note 24.—*Laminaria saccharina* var. *latissima* Turn. (p. 243).

Omitted from this list because Turner (1808) records that only one specimen was found and that was washed up, so that a storm may have brought it from outside the area.

I am very grateful to Dr. H. Hamshaw Thomas, who has not only acted as intermediary for me whilst I was in America, but who also gave me much valuable advice and criticism about the subject-matter, and who transmitted to me Mr. A. D. Cotton's comments, to whom I am likewise much indebted.

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Contributions towards the fungus flora of Uganda.—I. The Meliolinaceae of
Uganda. By C. G. HANSFORD, M.A., F.L.S., Plant Pathologist, Uganda
Department of Agriculture.

[Read 28 October 1937]

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THE following pages contain a complete list, as far as it is possible to ascertain, of all the fungi of this group so far collected in Uganda. Many of the specimens referred to in the text were forwarded to the late Prof. F. L. Stevens, who kindly verified the determinations in some instances, and in others suggested that they be described as new species.

I am indebted to Miss E. M. Wakefield, of the staff of the Kew Herbarium, for her aid and advice, and especially for revision of the manuscript. The type-specimens of the species and varieties described as new in this paper are all deposited in the Herbarium of the Royal Botanic Gardens, Kew.

AMAZONIA Theiss. in Ann. Myc. xi, p. 499 (1913).

1. AMAZONIA ASTERINOIDES (Wint.) Theiss. in Ann. Myc. xi, p. 499 (1913).
[3101.3240*.]

On leaves of a Rubiaceous shrub, Butambala, *Hansford 1368*.

2. AMAZONIA DIOSCOREAE Hansford et Stevens, sp. n. [3101.4240.]

Plagulae amphigenae, atrae, densae, orbiculares, 1·5–3·0 mm. diam. *Mycelium* ex hyphis brunneis rectiusculis vel undulatis alternatim vel irregulariter ramosis anastomosantibus 6–8 μ crassis septatis (articulis 12–18 μ longis) compositum. *Hyphopodia* capitata alternata, stipitata, 15–19 μ longa, cellula apicali subglobosa rarius sub-lobata vel angulata 9–13 μ longa et 6–13 μ lata, cellula basali 3–7 μ longa. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, ampullacea, 12–18 \times 6–9 μ . *Setae* nullae. *Perithecia* dimidiata, radiata, 250–350 μ diam., ex hyphis rectis 5–7 μ latis septatis (articulis 10 μ longis) composita, margine fimbriato. *Asci* bispori. *Sporae* brunneae, 4-septatae, cylindraceae, utrinque rotundatae, constrictae, 40–44 \times 14–18 μ .

Hab. in foliis *Dioscoreae* sp., Masaka Road, mile xi, Entebbe District, Uganda, *Hansford 1346*.

The colonies consist of an almost solid plate of hyphae and hyphopodia. Also collected in Butambala County, *Hansford 1372*.

* The numerals in square brackets which follow the scientific names here, and throughout this paper, refer to Professor F. L. Stevens's modification of the Beeli formula, introduced in Ann. Myc. xxv, p. 408 (1927).

3. AMAZONIA PEREGRINA Syd. in Ann. Myc. xv, p. 238 (1917). [3101.4230.]

On *Maesa lanceolata*, Kampala, *Hansford 1301*; Kyagwe, *Hansford 1356*, p.p.; Butambala, *Hansford 1416*, p.p.; Entebbe Road, *Hansford 1754*; Kampala, *Hansford 1988*.

This is usually found in moist situations and is often accompanied on the same leaves by *Meliola Groteana* Syd.

4. AMAZONIA UGANDENSIS Hansford, sp. n. [3101.5240.]

Plagulae amphigenae, rarius hypophyllae et caulincolae, 1-3 mm. diam., atrae, orbiculares, densissimae. *Mycelium* ex hyphis atro-brunneis radiatis 7-8 μ crassis septatis (articulis 11-19 μ longis) alternatim ramosis fere rectis compositum. *Hyphopodia capitata* alternata, numerosa, saepe compressa et elongata, cellula basali cylindraceo-conoidea 5-10 μ longa, cellula apicali ovata vel lato-rotundata 10-13 \times 8-10 μ . *Hyphopodia mucronata* non visa. *Perithecia* dimidiata, usque 350 μ diam., atra, sparsa. *Asci* 2-spori, fugaces. *Sporae* cylindraceae, atro-brunneae, utrinque rotundatae, constrictae, 4-septatae, 46-55 \times 15-17 μ .

Hab. in foliis *Piperis guineensis*, Kampala, *Hansford 1990*.

IRENE Theiss. & Syd. in Ann. Myc. xv, p. 194 (1917).

1. IRENE CALOSTROMA (Desm.) v. Hohnel in Ann. Myc. xvi, p. 213 (1918). [2201.4230.]

On *Rubus* sp., Kampala, *Hansford 774*; Bombo Road, *Hansford 1087, 1796*; Masaka Road, mile xiii, *Hansford 1339*.

2. IRENE INERMIS (Kalchbr. & Cooke) Theiss. & Syd. in Ann. Myc. xv, p. 194 (1917).

Var. MINOR Hansford et Stevens, var. nov. [3201.3230.]

Plagulae epiphyllae, rarius hypophyllae, 1-3 mm. diam., numerosissimae, saepe confluentes, atrae. *Mycelium* ex hyphis brunneis undulatis reticulatis alternatim ramosis septatis (articulis 18-25 μ longis) 6.5-8.5 μ crassis compositum. *Hyphopodia capitata* alternata, stipitata, 19-27 μ longa, cellula basali cylindracea vel cylindraceo-conoidea, cellula apicali ovoidea vel subglobosa 12-17 \times 9-12.5 μ . *Hyphopodia mucronata* haud numerosa, inter hyphopodia capitata interspersa, praecipue in centro plagularum evoluta, opposita, ampullacea, collo brevi, 13-18 μ longa. *Setae* nullae. *Perithecia* in centro plagularum laxe gregaria, atra, globosa, verrucosa, 180-230 μ diam., 4-6 setis larviformibus atris opacis rectis vel curvulis cylindraceis vel subconicis 35-57 μ longis 15-20 μ latis septatis constrictis superne ornata. *Asci* bispori. *Sporae* brunneae, 4-septatae, cylindraceae, leniter constrictae, utrinque late rotundatae, 40-45 \times 17-20 μ .

Hab. in foliis *Labiatarum* speciei indet., Kampala, *Hansford 1076* (type).

Differs from the type of the species as described by Doidge in 'Bothalia,' II, 432 (1928), chiefly in the alternate (occasionally opposite) branching of the mycelium, smaller perithecia, and smaller spores.

Also collected on *Coleus* sp., Entebbe Road, *Hansford 1134*, and on *Hyptis pectinata*, Kampala, *Hansford 1330*.

3. *IRENE NATALENSIS* Doidge in South African Journ. Nat. Hist. II, p. 40 (1920). [2203.4230.]

On *Dovyalis macrocalyx*, Entebbe Road, *Hansford 1941*.

4. *IRENE PEGLERAE* Doidge in South African Journ. Nat. Hist. II, p. 40 (1920). [3201.3220.]

On an undetermined shrub, Gayaza Road, *Hansford 992*.

IRENOPSIS Stevens in Ann. Myc. xxv, p. 411 (1927).

1. *IRENOPSIS BOSCIAE* (Doidge) Stevens in Ann. Myc. xxv, p. 435 (1927). [3401.4220.]

On *Capparis Afzelli*, Entebbe Road, *Hansford 1540*.

2. *IRENOPSIS CORONATA* (Speg.) Stevens, var. *TRIUMFETTÆ* Stevens in Ann. Myc. xxvi, p. 435 (1927). [3401.4220.]

On *Hibiscus* sp., Kampala, *Hansford 1263*; on *H. gossypinus*, Kyagwe, *Hansford 1360*; Butambala country, *Hansford 1415*; common.

3. *IRENOPSIS CORONATA* (Speg.) Stevens, var. *VANDERYSTII* (Beeli) Stevens in Ann. Myc. xxvi, p. 436 (1927). [3301.4220.]

On *Honckenya* sp., Entebbe Road, *Hansford 1851*; on *Hibiscus* sp., Kyagwe, *Hansford 1932*.

4. *IRENOPSIS CORONATA* (Speg.) Stevens, var. *HIBISCI* Hansford, var. nov. [3401.3220.]

Plagulae amphigenae, plerumque epiphyllae, effusae, tenues, atrae, saepe confluente majores. *Mycelium* ex hyphis undulatis 7–8 μ crassis septatis (articulis 20–35 μ longis) opposite vel irregulariter ramosis atro-brunneis compositum. *Hyphopodia capitata* alternata, 16–23 μ longa, cellula apicali lobata 12–17 μ longa et 12–15 μ lata, cellula basali cylindracea 3–6 μ longa. *Hyphopodia mucronata* opposita, praecipue in centro plagularum evoluta, inter hyphopodia capitata interspersa, ampullacea vel conoidea. *Perithecia* globosa, atra, verrucosa, setis 4–6 superne ornata; setae curvulae, acutae, atrae, 65–120 μ longae, basi 7–8 μ crassae. *Perithecia* 120–160 μ diam. *Sporae* cylindraceae, utrinque late rotundatae, 4-septatae, constrictae, atro-brunneae, 31–38 \times 11–13 μ .

Hab. in foliis *Hibisci* sp., Entebbe Road, *Hansford 1544*.

Differs from type chiefly in lobed capitate hyphopodia and smaller spores.

5. IRENOPSIS LEEAE Hansford, sp. n. [3402/3.3220.]

Plagulae hypophyllae, atrae, tenues, orbiculares, usque 3 mm. diam., saepe confluenta majores, irregulares. *Mycelium* ex hyphis undulatis brunneis septatis (articulis 17–25 μ longis) opposite vel irregulariter ramosis 6–8 μ crassis compositum. *Hyphopodia capitata* opposita, rarius unilateralia, in greges (10–12) disposita, 15–20 μ longa, cellula basali 2–6 μ longa, cellula apicali ovoidea vel irregulariter lobata 11–15 μ longa et 11–20 μ lata. *Hyphopodia mucronata* numerosa, alternata vel opposita, ampullacea, collo curvato, 14–23 μ longa et 7–10 μ lata. *Perithecia* sparsa, globosa, 120–160 μ diam., atra, verrucosa, setis erectis 9–15 superne ornata; setae curvulae atrae, 120–160 μ longae, 7–9 μ crassae, basi opacae, leniter attenuatae, apice acutae. *Ascii* bispori. *Sporae* 4-septatae, brunneae, cylindraceae, utrinque late rotundatae, leniter constrictae, 31–35 \times 12–14 μ .

Hab. in foliis *Leeae guineensis*, Masaka Road, Uganda, *Hansford 1342.*

The distribution of the hyphopodia is extremely characteristic, the capitate hyphopodia are in close groups of 5 or 6 pairs with long intervals between the groups; a few mucronate hyphopodia are found in the intervals and are restricted to such positions on the hyphae.

IRENINA Stevens in Ann. Myc. xxv, p. 411 (1927).

1. IRENINA ATRA (Doidge) Stevens in Ann. Myc. xxv, p. 467 (1927). [3101.5320.]

On *Piper* sp., Kyagwe, *Hansford 1938*; on *P. guineense*, near Kampala, *Hansford 1990.*

2. IRENINA BERSAMAE Hansford, sp. n. [3101.6330.]

Plagulae epiphyllae, atrae, 1–2 mm. diam. *Mycelium* ex hyphis atro-brunneis flexuosis unilateraliter ramosis septatis (articulis 30–35 μ longis) anastomosantisibus 10–11 μ crassis compositum. *Hyphopodia capitata* alternata, stipitata, 35–45 μ longa, cellula basali cylindracea 15 μ longa 10–12 μ lata, cellula apicali lobata irregulare 22–32 μ longa 25–35 μ lata. *Hyphopodia mucronata* numerosa, praecipue in centro plagularum evoluta, ampullacea, circa 25 \times 8 μ . *Perithecia* globosa, atra, verrucosa, 220–280 μ diam., in centro plagularum laxe gregaria. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, curvatae, constrictae, 4-septatae, 58–65 \times 22–28 μ .

Hab. in foliis *Bersamae* sp., Masaka Road, *Hansford 1783.*

3. IRENINA CYCLOPODA (Stev.) Stevens in Ann. Myc. xxv, p. 452 (1927). [3101.3220.]

On an undetermined Composite, Kampala, *Hansford 1328.*

4. IRENINA ENTEBBEENSIS Hansford et Stevens, sp. n. [3101.4230.]

Plagulae epiphyllae, densae, atrae, orbiculares, usque 4 mm. diam. *Mycelium* ex hyphis brunneis rectiusculis vel leniter undulatis septatis (articulis

$17\text{--}25 \mu$ longis) alternatim ramosis anastomosantibus $8\text{--}9 \mu$ crassis compositum. *Hyphopodia capitata* numerosa, $20\text{--}30 \mu$ longa, alternata, recta vel curvata, cellula basali $5\text{--}10 \mu$ longa, cellula apicali rotundata recurvata vel irregulariter lobata $13\text{--}22 \times 10\text{--}16 \mu$. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, opposita vel unilateralia, plus minusve lageniformia, $18\text{--}23 \mu$ longa, basi 7μ lata, in collum curvatum $3\text{--}4 \mu$ crassum attenuata. *Setae* nullae. *Perithecia* sparsa, atra, globosa, verrucosa, $180\text{--}220 \mu$ diam. *Sporae* 4-septatae, brunneae, cylindraceae, utrinque late rotundatae, constrictae, $42\text{--}49 \times 17\text{--}19 \mu$.

Hab. in foliis *Alchorneae* sp., Butambala, Uganda, *Hansford* 1369 (type); in foliis *Macarangae* sp., Entebbe Road, *Hansford* 1439.

5. *IRENINA GLABRA* (B. & C.) Stevens in Ann. Myc. xxv, p. 461 (1927). [3101.4230.]

On Coffee, *Small* 606; *Coleus* sp., *Dummer* 2340; *Hansford* 1357; undetermined Labiate, *Dummer* 2860; *Vernonia* sp., *Hansford* 985; *Wedelia* sp., *Hansford* 750, 1336.

6. *IRENINA GYMNOспорIAE* (H. & P. Syd.) Stevens in Ann. Myc. xxv, p. 467 (1927). [3101.3220.]

On *Gymnosporia senegalensis*, Kyagwe, *Dummer* 2510.

7. *IRENINA HANSFORDII*, Stevens, sp. n. [3101.3210.]

Plagulae epiphyllae, atrae, tenues, orbicularis, 1–2 mm. diam. *Mycelium* ex hyphis brunneis undulatis septatis (articulis $18\text{--}27 \mu$ longis) opposite ramosis anastomosantibus $6\text{--}8 \mu$ crassis compositum. *Hyphopodia capitata* alternata, $17\text{--}25 \mu$ longa, cellula basali $3\text{--}8 \mu$ longa et $6\text{--}8 \mu$ crassa, cellula apicali subglobosa vel irregulariter lobata $13\text{--}17 \mu$ longa et $12\text{--}17 \mu$ lata. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, alternata vel rarius opposita, tenui ampullacea, $15\text{--}19 \mu$ longa, in collum rectum vel curvatum attenuata. *Setae* nullae. *Perithecia* in centro plagularum laxe gregaria, atra, globosa, verrucosa, $60\text{--}100 \mu$ diam. *Asci* bispori. *Sporae* 4-septatae, brunneae, cylindraceae, utrinque late rotundatae, leniter constrictae, $35\text{--}40 \times 13\text{--}16 \mu$.

Hab. in foliis *Acalyphe* sp., Nakifuma, Uganda, *Hansford* 1197 (type); Kyagwe, *Hansford*, 1404.

The fungus is commonly found in shady places and usually the colonies are scattered among those of *Asterina tenuis*.

8. *IRENINA IRREGULARIS* (Stev.) Stevens in Ann. Myc. xxv, p. 455 (1927). [3101.4220.]

On *Justicia* sp., Entebbe Road, *Hansford* 1252, 1460; on *Mimulopsis* sp., Butambala, *Hansford* 1417.

9. *IRENINA LAGUNCULARIAE* (Earle) Stevens in Ann. Myc. xxv, p. 458 (1927). [3101.3220.]

On *Combretum* sp., Entebbe, *Hansford* 1874.

10. IRENINA MELASTOMACEARUM (Speg.) Stevens in Ann. Myc. xxv, p. 459 (1927). [3101.3220.]

On *Dissotis* sp., Dummer 1103; Butambala, Hansford 1410; Kyagwe, Hansford 1535.

11. IRENINA sp. near *obesa* (Speg.) Stevens in Ann. Myc. xxv, p. 450 (1927). [3103.4230.]

On *Ficus* sp., Butambala, Hansford 1409.

MELIOLA Fries in Syst. orb. veg. p. 111 (1825).

1. MELIOLA BAKERI H. & P. Syd. in Ann. Myc. xiv, p. 355 (1916). [3113.4222.]

On *Vitaceae* indet., Kyagwe, Hansford 1930.

2. MELIOLA BERSAMAE Hansford, sp. n. [3111.5342.]

Plagulae amphigenae, atrae, orbiculares, 2–5 mm. diam., densae, subcrustosae. *Mycelium* ex hyphis atro-brunneis leniter undulatis septatis (articulis 12–16 μ longis) opposite vel unilateraliter ramosis anastomosantibus 7–8 μ diam. compositum. *Hypopodia capitata* alternata, numerosa, 20–32 μ longa, cellula basali 7–11 μ longa, cellula apicali lobata vel irregulare 15–22 μ longa et 10–15 μ lata saepe recurvata. *Hypopodia mucronata* haud numerosa, opposita, ampullacea, praecipue in centro plagularum evoluta. *Setae myceliales* numerosae, erectae, rectae vel leniter curvatae, 250–360 μ longae, atro-brunneae, basi opacae, 7–9 μ crassae, apice acutae. *Perithecia* sparsa, atra, 190–360 μ diam., sub-globosa, verrucosa. *Asci* 2-spori, fugaces. *Sporae* ellipsoideae vel cylindraceae, 4-septatae, constrictae, atro-brunneae, 50–55 \times 20–22 μ .

Hab. in foliis *Bersamae* sp., Entebbe Road, Uganda, Hansford 1747.

3. MELIOLA BERSAMICOLA Hansford, sp. n. [3111.5232.]

Plagulae amphigenae sed plerumque epiphyllae, atrae, orbiculares, 2–5 mm. diam., velutinae. *Mycelium* ex hyphis atro-brunneis rectis septatis (articulis 25–35 longis) anastomosantibus opposite vel unilateraliter ramosis 10–11 μ crassis compositum. *Hypopodia capitata* alternata, numerosa, 20–28 μ longa, cellula basali 5–7 μ longa et 10–11 μ lata, cellula apicali rotundata vel globosa 15–20 μ longa et 14–17 μ lata. *Setae myceliales* 240–360 μ longae, atrae, numerosissimae, basi opacae, 10–12 μ crassae, apice acutae. *Perithecia* globosa, atra, verrucosa, sparsa, 180–220 μ diam. *Sporae* atro-brunneae, cylindraceae utrinque rotundatae, 4-septatae, constrictae, 50–56 \times 14–17 μ .

Hab. in foliis *Bersamae* sp., Masaka Road, Hansford 1783.

4. MELIOLA BICORNIS Wint. in Hedwigia, xxv, p. 99 (1886). [3133.4221.]

On *Glycine javanica*, Dummer 918, 4270; Small 123; on *Teramnus labialis* Kyagwe, Dummer 2869; on *Albizzia Brownei*, Bombo Road, Hansford 756; Entebbe Road, Hansford 1287; on *Eriosema* sp., Bombo Road, Hansford 761;

on *Gliricidia sepium*, Kampala, *Hansford 986*; *Hansford 1811*; on *Desmodium* sp., Kampala, *Hansford 1144*; Jinja Road, *Hansford 1764*; on *Crotalaria* sp., Kampala, *Hansford 1832*; on *Albizia* sp., Entebbe Road, *Hansford 1947*; on *Erythrina tomentosa*, Kyagwe, *Hansford 1961*; Gayaza, *Hansford 1171*.

5. **MELIOLA BICORNIS** Wint. var. **GALACTIAE** Stevens in Illinois Biol. Monogr. II, p. 65 (1916). [311/33.4222.]

On *Desmodium* sp., Masaka Road, *Hansford 1955*.

6. **MELIOLA BICORNIS** Wint. var. **TEPHROSIAE** Beeli in Bull. Jard. Bruxelles, VIII, p. 1 (1923). [3131.3223.]

On *Tephrosia* sp., Kampala, *Hansford 1264*.

7. **MELIOLA BIDENTATA** Cooke in Grevillea, XI, p. 37 (1882). [3131.4221.]

On *Kigelia moosa*, Dummer 2829. (?) On an unknown host, Mukono Forest, *Hansford 1969*.

8. **MELIOLA CARDIOSPERMI** Hansford et Stevens, sp. n. [3112.4222.]

Plagulae epiphyllae et caulicolae, orbiculares, atrae, 1–4 mm. diam., densae, velutinae. *Mycelium* ex hyphis brunneis plus-minusve rectis septatis (articulis 20–25 μ longis) opposite ramosis 8–9 μ crassis compositum. *Hypopodia capitata* opposita, rarius alternata, numerosa, 13–19 μ longa, cellula basali brevi 2–5 μ longa, cellula apicali rotundata subglobosa vel subangulata 11–13 μ longa et 11–14 μ lata. *Hypopodia mucronata* inter hypopodia capitata interspersa, ampullacea, haud numerosa, opposita, in collum curvatum attenuata. *Setae myceliales* numerosissimae, rectae, atrae, opacae, simplices, 270–330 μ longae, basi 8–10 μ crassae, apice acutae, rarius obtusae. *Perithecia* atra, globosa, verrucosa, gregaria, 150–180 μ diam. *Asci* bispori. *Sporae* brunneae, ellipsoideae vel sub-cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 39–42 \times 16–19 μ .

Hab. in foliis caulinibusque *Cardiospermum* sp., Masaka Road, Uganda, *Hansford 1323* (type); *Hansford 1473*.

The crowded hypopodia and branched hyphae form almost a solid plate of tissue. Common on this host throughout the Lake Victoria area of Uganda.

9. **MELIOLA CHANDLERI** Hansford, sp. n. [3141.4221.]

Plagulae epiphyllae, usque 3 mm. diam., atrae, orbiculares, velutinae, densae. *Mycelium* ex hyphis undulatis 7–8 μ crassis septatis (articulis 18–23 μ longis) unilateraliter ramosis atro-brunneis compositum. *Hypopodia capitata* numerosa, alternata vel unilateralia, 20–26 μ longa, cellula apicali lobata 15–19 μ longa et 10–18 μ lata, cellula basali 6–10 μ longa curvata. *Hypopodia mucronata* rarissima, inter hypopodia capitata interspersa, alternata vel opposita, ampullacea. *Setae myceliales* numerosae, 220–260 μ longae, 7–10 μ crassae, atrae, apice 1–2-dichotomae, ramis curvatis reflexis usque ad 28 μ longis, ramulis 6–10 μ longis, saepe bidentatis. *Perithecia* sparsa, atra, globosa, verrucosa,

160–190 μ diam. *Sporae* atro-brunneae, cylindraceae utrinque rotundatae, 4-septatae, 38–43 \times 14–15 μ , constrictae.

Hab. in foliis *Acalyphae* (? *A. fruticosae*), Entebbe Road, *Hansford* 1827.

10. *MELIOLA CISSAMPELI* Hansford et Stevens, sp. n. [3131.4222.]

Plagulae orbiculares, epiphyllae, tenues, usque 5 mm. diam. *Mycelium* ex hyphis brunneis rectis vel plus-minusve undulatis septatis (articulis 20–30 μ longis) opposite ramosis 5–7 μ crassis compositum. *Hypopodia capitata* alternata, rarius opposita, numerosa, 13–17 μ longa, cellula basali 3–6 μ longa, cellula apicali rotundata vel ovata 9–13 μ longa et 8–12 μ lata. *Hypopodia mucronata* inter hypopodia capitata interspersa, praecipue in centro plagularum evoluta, ampullacea, 15–20 μ longa, basi 6–8 μ crassa, collo brevi. *Setae myceliales* rectae, atrae, 270–360 μ longae, basi 7–9 μ crassae, rarissime simplices, acutae, plerumque ad apicem subtorulosae, dentatae, dentibus brevibus acutisque ad 10 μ longis rarius ad 30 μ . *Perithecia* atra, globosa, verrucosa, sparsa, 140–180 μ diam. *Asci* bispori. *Sporae* brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 36–40 \times 12–15 μ .

Hab. in foliis *Cissampeli mucronatae*, Entebbe Road, Uganda, *Hansford* 1521.

11. *MELIOLA CISSI* Hansford, sp. n. [3133.4223.]

Plagulae epiphyllae et caulinæ, tenues, atrae, usque ad 5 mm. diam., orbiculares, velutinae. *Mycelium* ex hyphis atro-brunneis undulatis 7–8 μ crassis septatis (articulis 20–40 μ longis) opposite ramosis compositum. *Hypopodia capitata* alternata vel opposita, numerosa, 20–30 μ longa, cellula apicali clavata 14–19 μ longa et 11–14 μ lata, cellula basali curvata 5–11 μ longa. *Hypopodia mucronata* inter hypopodia capitata interspersa, praecipue in centro plagularum evoluta, ampullacea, collo curvato. *Setae myceliales* numerosae, atrae, erectae, opacae, rectae, irregulariter ramosae vel dentatae (ad 30 μ), 280–600 μ longae, basi 11–14 μ crassae. *Perithecia* sparsa, atra, globosa, verrucosa, 160–200 μ diam. *Asci* 2-spori, fugaces. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, leniter curvatae, 4-septatae, constrictae, 45–48 \times 14–19 μ .

Hab. in foliis *Cissi* sp., Masaka Road, *Hansford* 1956.

12. *MELIOLA CLAVULATA* Wint. in *Hedwigia*, xxv, p. 98 (1886). [3111.3221.]

On *Ipomoea* sp., Dummer 2371; on *Convolvulaceæ* indet. Dummer 1483.

Miss E. M. Wakefield has kindly re-examined these specimens and states that both have two species of *Meliola* on them, the present fungus being accompanied by *M. malacotricha*.

13. *MELIOLA CLERODENDRI* Hansford, sp. n. [3133.3222.]

Plagulae epiphyllae, rarius hypophyllae, atrae, orbiculares, velutinae, 1–3 mm. diam. *Mycelium* ex hyphis atro-brunneis 7–8 μ crassis septatis (articulis 25–40 μ longis) opposite ramosis compositum. *Hypopodia capitata*

alternata vel opposita, 12–17 μ longa, cellula basali breviter cylindracea 4–6 μ longa, cellula apicali rotundata curvulata 8–14 μ longa et 10–14 μ lata. *Hyphopodia mucronata* inter hyphopodia capitata interspersa in centro plagularum, ampullacea. *Setae myceliales* numerosae, rectae, atrae, erectae, septatae, apice dentatae (ad 15 μ), 280–440 μ longae, basi 8–9 μ crassae. *Perithecia* sparsa, globosa, atra, verrucosa, 120–160 μ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 35–39 \times 10–11 μ .

Hab. in foliis *Clerodendri* sp., Masaka Road, *Hansford 1792.*

14. *MELIOLA CLERODENDRICOLA* P. Henn. in *Hedwigia*, xxxvii, p. 288 (1895).
[3111.3221.]

On leaves of *Clerodendron* spp., *Maitland* 229, 271; *Small* 461, *Dummer* 3014, *Hansford* 1757; common.

15. *MELIOLA COFFEAE* Hansford, sp. n. [3131.3221.]

Plagulae tenues, atrae, orbiculares, hypophyllae, usque 5 mm. diam., sparsae. *Mycelium* ex hyphis atro-brunneis undulatis 6 μ crassis septatis (articulis 25–30 μ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata, 13–18 μ longa, cellula apicali rotundata saepe curvata 9–12 \times 9–10 μ , cellula basali saepe curvata 5–7 μ longa. *Hyphopodia mucronata* haud numerosa, inter hyphopodia capitata interspersa, opposita vel alternata, curvata, ampullacea. *Setae myceliales* atrae, rectae, septatae, opacae, apice acutae, 2–4-dentatae (ad 14 μ) 140–300 \times 7 μ . *Perithecia* atra, globosa, sparsa, verrucosa, 100–190 μ diam. *Sporae* atro-brunneae, cylindraceae utrinque rotundatae, 4-septatae, constrictae, 34–37 \times 11–13 μ .

Hab. in foliis *Coffea robustae*, Kampala, Uganda, *Hansford 1835.*

A few colonies of this *Meliola* were found scattered among numerous colonies of *Irenina glabra*.

16. *MELIOLA DEINBOLLIAE* Hansford, sp. n. [3111.4222.]

Plagulae epiphyllae, numerosae, atrae, orbiculares, tenues, saepe confluentes. *Mycelium* ex hyphis atrobrunneis undulatis 7–9 μ crassis septatis (articulis 18–27 μ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata, numerosa, 18–23 μ longa, cellula apicali irregulariter sub-lobata saepe curvata vel reflexa 12–17 \times 9–15 μ , basali 4–7 μ longa. *Hyphopodia mucronata* alternata vel opposita, ampullacea vel lageniformia, collo brevi curvato, inter hyphopodia capitata interspersa. *Setae myceliales* numerosae, erectae, atrae, ad apicem torulosae, acutae, rarissime dentatae (ad 8 μ), 180–370 \times 8–10 μ . *Perithecia* sparsa, 140–170 μ diam., atra, globosa, verrucosa. *Sporae* cylindraceae, utrinque rotundatae, 4-septatae, constrictae, atro-brunneae, 37–41 \times 12–15 μ .

Hab. in foliis *Deinbolliae fulvo-tomentosae*, Entebbe Road, Uganda, *Hansford 1950.*

17. **MELIOLA DRACAENICOLA** Pat. & Har. in Bull. Soc. Myc. France, **xxiv**, p. 14 (1908). [3141.4231.]

On *Dracaena ugandensis* Nkokonjeru, Bugishu, *Hansford 794*; common in damp and shady places in forests all over Uganda.

18. **MELIOLA DUGGENAE** Stevens in Ann. Myc. **xxvi**, p. 198 (1928).

Var. **MAJOR** Hansford, var. nov. [311/31.3222.]

Plagulae atrae, orbiculares, plerumque hypophyllae, usque ad 5 mm. diam., velutinae, tenues. *Mycelium* ex hyphis leniter undulatis atro-brunneis 6–7 μ crassis septatis (articulis 25–35 μ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata vel unilateralia, saepe curvata, 18–22 μ longa, cellula basali cylindracea 5–7 μ longa, cellula apicali ovata vel rotundata 12–15 μ longa et 10–12 μ lata. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, saepius alternata, numerosa, ampullacea, collo tenui. *Setae myceliales* numerosae, sparsae, 160–320 μ longae, apice bifurcatae vel 2–3-dentatae (ad 25 μ), dentibus obtusis, rarius simplices et acutae. *Perithecia globosa*, atra, verrucosa, sparsa, 100–140 μ diam. *Sporae* atro-brunneae, cylindraceae utrinque rotundatae, 4-septatae, constrictae, 35–39 \times 13–16 μ .

Hab. in foliis *Rubiacearum* sp. indet., Mukono Forest, Kyagwe, Uganda, *Hansford 1970*.

Differs from the type chiefly in longer setae and larger spores.

19. **MELIOLA EKEBERGIAE** Hansford, sp. n. [3112.3221.]

Plagulae epiphyllae, atrae, numerosae, saepe confluentes, 2–3 mm. diam., densae, crustosae. *Mycelium* ex hyphis atro-brunneis 7–8 μ crassis septatis (articulis 17–30 μ longis) opposite ramosis compositum. *Hyphopodia capitata* opposita vel unilateralia, numerosissima, 17–22 μ longa, cellula apicali cylindracea-ovata 11–15 μ longa et 6–9 μ lata, cellula basali 4–7 μ longa. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, praecipue in centro plagularum evoluta, opposita, ampullacea. *Perithecia* sparsa, atra, globosa, verrucosa, 120–160 μ diam. *Sporae* atro-brunneae, 4-septatae, cylindraceae, utrinque rotundatae, constrictae, 34–37 \times 14–16 μ . *Setae myceliales* numerosae, erectae, atrae, septatae, 170–260 μ longae, basi 8–9 μ crassae, simplices, apice acutae.

Hab. in foliis *Ekebergiae* sp., Entebbe Road, Uganda, *Hansford 1828, 1842*.

20. **MELIOLA FICIUM**, Yates in Philippine Journ. Sci., C. Bot. **xiii**, p. 368 (1918). [3111.4223.]

On *Ficus* sp., Butambala, *Hansford 1409* (det. F. L. Stevens).

21. **MELIOLA FUNTUMIAE** Beeli in Bull. Jard. Bot. Bruxelles, **vii**, p. 95 (1920). [3111.4222.]

On *Apocynaceae* indet., Entebbe Road, *Hansford 1522*.

22. **MELIOLA FUNTUMIAE** Beeli, var. **HAMATA** Hansford et Stevens, var. nov.

Plagulae amphigenae, tenues, atrae, 2–7 mm. diam., saepe confluentes. *Mycelium* ex hyphis brunneis plus-minusve undulatis septatis (articulis 20–30 μ

longis) opposite ramosis 7–8 μ crassis compositum. *Hyphopodia capitata* cylindracea, recta vel curvata, alternata vel unilateralia, 15–20 μ longa, cellula apicali rotundata 12–14 μ longa et 8–10 μ lata, cellula basali 3–6 μ longa. *Hyphopodia mucronata* praecipue in centro plagularum evoluta, numerosa, opposita, ampullacea, collo brevi. *Setae myceliales* praecipue juxta perithecia dispositae, atro-brunneae, ad apicem obtusum pellucidum hamatum leniter attenuatae, simplices, 270–450 μ longae et basi 10 μ latae. *Perithecia* 140–160 μ diam., globosa, atra, verrucosa, sparsa, sicco collapsa. *Asci* bispori, fugaces. *Sporae* brunneae, cylindraceae, utrinque rotundatae, 4-septatae, leniter constrictae, 39–47 \times 13–18 μ .

Hab. in foliis *Funtumiae elasticae*, Butambala, Uganda, *Hansford 1408* (type); Kyagwe, *Hansford 1433*.

Differs from type in appearance of colonies and chiefly in its hamate setæ.

23. *MELIOLA FURCILLATA* Doidge in Trans. Roy. Soc. South Africa, v, p. 738 (1917). [311/31.4223.]

On *Schmidelia* sp., Masaka Road, *Hansford 1338*; on *Sapindaceae* indet., Entebbe Road, *Hansford 1440*.

(No. 1338 differs from the description given by Doidge in that the hyphae are 8–9 μ wide, cells 20–27 μ long, mycelial setae 280–570 μ long, with apex rough or shortly 2–3-dentate, occasionally acute and simple; colonies velvety; perithecia 100–150 μ diam., crowded in a central group; spores 39–43 \times 14–16 μ .)

24. *MELIOLA GENICULATA* Syd. & Butl. in Ann. Myc. ix, p. 381 (1911). [3131.3221.]

On *Rhus* sp., Dummer 1321 (this record is doubtful, and the specimen may be *M. Anacardii* Zimm., according to Miss E. M. Wakefield, who has recently re-examined this material).

25. *MELIOLA GROTEANA* H. & P. Syd. in Ann. Myc. xi, p. 402 (1913). [3113.4222.]

On *Maesa* sp., Gayaza, *Hansford 1173*; Masaka Road, *Hansford 1349*; Kyagwe, *Hansford 1356*; very common in the wetter districts of Uganda.

26. *MELIOLA JASMINI* Hansford et Stevens, sp. n. [3411.3211.]

Plagulae 2–5 mm. diam., saepe confluentes et tunc totam fere paginam folii occupantes, epiphyllae, tenues, atrae. *Mycelium* ex hyphis rectis opposite ramosis atro-brunneis anastomosantibus septatis (articulis 27–30 μ longis) 6–6½ μ crassis compositum. *Hyphopodia capitata* alternata, 17–24 μ longa, cellula basali 4–8 μ longa, cellula apicali ovata vel subglobosa 12–17 μ longa et 8–12 μ lata. *Hyphopodia mucronata* numerosa, opposita, 13–17 μ longa, ampullacea, collo brevi curvato. *Setae myceliales* haud numerosae, sparsae, atrae, subrectae, simplices, 170–250 μ longae, basi 8 μ crassae, apice acutae. *Perithecia* atra, globosa, verrucosa, 140–180 μ diam., basi setibus 4–7 ornata:

setae rectae, 170–280 μ longae, basi 8–9 μ crassae, apice acutae. Sporae 4-septatae, brunneae, cylindraceae utrinque late rotundatae, leniter constrictae, 33–36 \times 13–14 μ .

Hab. in foliis *Jasmini* sp., Entebbe Road, Uganda, *Hansford 1251.*

This species is common in the Lake Victoria region of Uganda, in wet places.

27. MELIOLA KAMPALENSIS Hansford, sp. n. [3121.3221.]

Plagulae atrae, orbiculares, densae, semi-crustosae, velutinae, amphigenae et petiolicolae, 1–4 mm. diam. *Mycelium* ex hyphis atro-brunneis leniter undulatis 6–8 μ crassis septatis (articulis circa 20 μ longis) opposite ramosis anastomosantibus compositum. *Hyphopodia capitata* numerosa, alternata vel unilateralia, 14–19 μ longa, cellula basali 3–6 μ longa, cellula apicali rotundata ovata vel sub-lobata 10–14 \times 7–9 μ . *Hyphopodia mucronata* inter hyphopodia capitata interspersa haud numerosa, ampullacea, opposita, collo brevi curvato. *Setae myceliales* numerosissimae, erectae, atrae, sursum curvatae vel hamatae, ad apicem obtusae (saepe sursum torulosae), 150–240 μ longae et basi 8–9 μ latae. *Perithecia* numerosa, gregaria, globosa, atra, verrucosa, 150–190 μ diam. *Asci* 2–4-spori, fugaces. Sporae cylindraceae, utrinque rotundatae, atro-brunneae, 4-septatae, leniter constrictae, 30–34 \times 12–13 μ .

Hab. in foliis *Markhamiae platycalycis*, Kampala, *Hansford 1385* (type); Entebbe, *Hansford 1875.*

28. MELIOLA KIBIRAE Hansford et Stevens, sp. n. [3111.3221.]

Plagulae epiphyllae et caulincolae, orbiculares, 1–3 mm. diam., tenues. *Mycelium* ex hyphis brunneis rectis septatis (articulis 20–35 μ longis) opposite ramosis 5–7 μ crassis compositum. *Hyphopodia capitata* alternata, 17–27 μ longa, recta, cellula basali cylindracea 5–13 μ longa, cellula apicali ovata vel rotundata 14–17 \times 9–12 μ . *Hyphopodia mucronata* praecipue in centro plagularum evoluta, opposita, ampullacea, 12–15 μ longa, basi 7–8 μ crassa, collo brevi curvato. *Setae myceliales* juxta perithecia gregatim (4–8) evolutae, atrae, rectae, 170–240 μ longae, basi 8–9 μ crassae, apice acutae. *Perithecia* globosa, atra, verrucosa, sparsa, 120–140 μ diam. Sporae brunneae, 4-septatae, leniter constrictae, cylindraceae, utrinque rotundatae, 30–34 \times 12–14 μ .

Hab. in foliis *Rubiacearum* sp. indet., Entebbe Road, Uganda, *Hansford 1475.*

Close to *M. Mitchellae*, but has shorter setae.

29. MELIOLA LANCEOLATO-SETOSA H. & P. Syd. in Ann. Myc. XII, p. 197 (1914). [3111.4232.]

On *Markhamia platycalyx*, Nagunga, Dummer 1112 (previously determined as *M. Pazschkeana* Gaill. in Kew Bull. 1920, p. 295); Small 293; *Hansford!* This is the commonest *Meliola* on this host in Uganda.

30. MELIOLA LANDOLPHIAE Hansford, sp. n. [311/33.3223.]

Plagulae epiphyllae, tenues, atrae, orbiculares, usque 5 mm. diam., velutinae. *Mycelium* ex hyphis atro-brunneis undulatis 6–7 μ crassis septatis (articulis

$22\text{--}35 \mu$ longis) opposite ramosis anastomosantibus compositum. *Hyphopodia capitata* opposita vel alternata, $14\text{--}20 \mu$ longa, cellula apicali cylindracea-clavata $8\text{--}14 \times 8\text{--}10 \mu$, cellula basali $3\text{--}7 \mu$ longa. *Hyphopodia mucronata* opposita, in centro plagularum evoluta. *Setae myceliales* rectae, atrae, numerosae, septatae, $240\text{--}420$ (-700) μ longae et basi 9μ crassae, simplices vel 2-4-dentatae, apice acutae. *Perithecia* sparsa, atra, globosa, verrucosa, $130\text{--}180 \mu$ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae constrictae, $34\text{--}38 \times 12\text{--}16 \mu$.

Hab. in foliis *Landolphiae* sp., Entebbe Road, *Hansford* 1853.

The capitate hyphopodia are often formed slightly behind the septa of the hyphae in this species, an unusual character in *Meliola*.

31. *MELIOLA LEPISTEMONIS* Hansford, sp. n. [3112.3222.]

Plagulae epiphyllae, atrae, minutae, usque 1 mm. diam., densae. *Mycelium* ex hyphis atrobrunneis $7\text{--}9 \mu$ crassis septatis (articulis $15\text{--}20 \mu$ longis) opposite ramosis rectis compositum. *Hyphopodia capitata* opposita, numerosa, $11\text{--}15 \mu$ longa, cellula apicali rotundata vel ovata $8\text{--}12 \times 7\text{--}9 \mu$, cellula basali $2\text{--}4 \mu$ longa. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, ampullacea, collo curvato. *Setae myceliales* haud numerosae, sparsae, erectae, atrobrunneae, simplices, rectae, $250\text{--}350 \mu$ longae, basi $8\text{--}9 \mu$ crassae, apice acutae. *Perithecia* atra, globosa, verrucosa, $150\text{--}180 \mu$ diam., in centro plagularum laxe gregaria. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, $33\text{--}40 \times 14\text{--}17 \mu$.

Hab. in foliis *Lepistemonis owariensis*, Entebbe Road, *Hansford* 1753.

32. *MELIOLA LONGISETA* v. Hohnel in Sitzber. K. Akad. Wiss. Wien, Math.-natur. Kl. cxvi, p. 100 (1907). [3111.4223.]

On *Psychotria* sp., Kampala, *Hansford* 1854.

33. *MELIOLA MAESICOLA* Hansford et Stevens, sp. n. [3113.4222.]

Plagulae hypophyllae, densae, orbiculares, 3-8 mm. diam., atrae. *Mycelium* ex hyphis brunneis leniter undulatis septatis (articulis $20\text{--}22 \mu$ longis) opposite vel unilateraliter ramosis $7\text{--}9 \mu$ crassis compositum. *Hyphopodia capitata* opposita, alternata vel unilateralia, $15\text{--}21 \mu$ longa, cellula basali $3\text{--}5 \mu$ longa, cellula apicali ovata vel cylindracea rotundata $12\text{--}16 \mu$ longa et $8\text{--}9 \mu$ lata. *Hyphopodia mucronata* ampullacea, $14\text{--}22 \mu$ longa, collo curvato. *Setae myceliales* numerosae, erectae, rectae, atro-brunneae, opacae, $340\text{--}420 \mu$ longae, inferne $7\text{--}8 \mu$ crassae, apicem versus leniter attenuatae, apice simplices acutae vel denticulatae (dentibus brevibus acutisque ad 8μ). *Perithecia* in centro plagularum laxe gregaria, atra, globosa, verrucosa, $160\text{--}180 \mu$ diam. *Asci* bispori. *Sporae* 4-septatae, brunneae, cylindraceae vel sub-ellipsoideae, utrinque late rotundatae, leniter constrictae, $41\text{--}45 \times 15\text{--}17 \mu$.

Hab. in foliis *Maesae* sp., Bombo Road, Kampala, *Hansford* 758.

The fungus is closely related to *M. furcillata*, but differs from the description

of the latter in being restricted to the lower surface of the host-leaf, in its denser colonies, the capitate hyphopodia being often opposite and the mucronate hyphopodia on separate branches of the mycelium. The mycelial setae do not approach the upper limit ($900\ \mu$) of those of *M. furcillata*.

34. *MELIOLA MALACOTRICA* Speg. in Ann. Soc. Cient. Argentina, xxvi, no. 59 (1888). [3113.3221.]

On *Ipomoea* spp., Hansford 990, 991, 772, 757 (?), 1667; very common.

35. *MELIOLA MARKHAMIAE* Hansford et Stevens, sp. n. [3111.3222.]

Plagulae amphigenae, atrae, velutinae, tenues, 2–5 mm. diam. Mycelium ex hyphis brunneis rectis septatis (articulis 25–33 μ longis) opposite ramosis anastomosantibus 6–7 μ crassis compositum. Hyphopodia capitata alternata vel unilateralia, 16–20 μ longa, cellula basali 4–7 μ longa, cellula apicali ovata 10–14 \times 7–9·5 μ . Hyphopodia mucronata opposita, inter hyphopodia capitata interspersa, ampullacea, collo curvato. Setae myceliales rectae, atrae, ad apicem sub-pellucidae, 260–350 μ longae, basi opacae et 7–9 μ crassae, apice acutae. Perithecia globosa, atra, verrucosa, 160–180 μ diam. Sporae brunneae, 4-septatae, leniter constrictae, cylindraceae, utrinque late rotundatae, 31–34 \times 11–14 μ .

Hab. in foliis *Markhamiae platycalycis*, Nyakafumu, Mengo District, Uganda, Hansford 1199.

36. *MELIOLA MICROSPORA* Pat. & Gaill. in Bull. Soc. Myc. France, iv, p. 104 (1888). [3111.2121.]

On *Hoslundia* sp., Kampala, Hansford 984, 1072; common.

37. *MELIOLA NEPHELII* Sacc. in Boll. Orto Bot. Univ. Napoli, vi, p. 42 (1921).

Var. *MAJOR* Hansford et Stevens, var. nov. [3113.34223.]

Plagulae epiphyllae, atrae, 1–3 mm. diam., tenues. Mycelium ex hyphis atro-brunneis 7–8 μ crassis septatis (articulis 15–20 μ longis) opposite ramosis rectiusculis compositum. Hyphopodia capitata alternata, rarius opposita, 17–20 μ longa, cellula basali cylindracea 2–5 μ longa, cellula apicali cylindracea vel ovata sursum rotundata 13–15 \times 7–9 μ . Hyphopodia mucronata opposita, inter hyphopodia capitata interspersa, numerosa, ampullacea, 16–23 \times 7–9 μ . collo brevi crasso curvato. Setae myceliales erectae, rectae, atro-brunneae. opacae, 250–650 μ longae, basi 8–9 μ crassae, apice obtusae vel 2–3-dentatae. Perithecia globosa, atra, verrucosa, 150–180 μ diam., sparsa. Ascii 2-spori. fugaces. Sporae atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae. constrictae, 36–40 \times 13–15 μ .

Hab. in foliis *Allophyli* sp., Entebbe Road, Hansford 1443.

Differs from type in its larger spores.

38. *MELIOLA MITCHELLAE* Cooke in Grevillea, vi, p. 143 (1878). [3111.3221.]

On *Pavetta* sp., Entebbe Road, Hansford 1752.

39. *MELIOLA MITCHELLAE* Cooke, var. *LONGISETA* Hansford, var. nov. [3111.3222.]

A typo setis differt :—setae 280–480 μ longae, basi 10–11 μ crassae, acutae, sursum saepe torulosae.

Hab. in foliis *Psychotriae nigropunctatae*, Entebbe Road, *Hansford 1939*.

40. *MELIOLA OLDENLANDIAE* Hansford et Stevens, sp. n. [3111.3222.]

Plagulae amphigenae, orbiculares, atrae, saepe confluentes, 1–4 mm. diam. *Mycelium* ex hyphis undulatis brunneis opposite ramosis septatis (articulis 20–30 μ longis) anastomosantibus 6–7 μ crassis compositum. *Hyphopodia capitata* alternata, 16–22 μ longa, cellula basali 3–6 μ longa, cellula apicali ovata vel sub-globosa 12–15 \times 12–13 μ . *Hyphopodia mucronata* opposita, haud numerosa, praecipue in centro plagularum evoluta, ampullacea. *Setae myceliales* erectae, rectae, atrae, ad apicem torulosae, sub-pellucidae, simplices, apice acutae, 200–360 μ longae, basi 9 μ crassae. *Perithecia* 120–150 μ diam., atra, globosa, verrucosa. *Sporae* brunneae, 4-septatae, leniter constrictae, cylindraceae, utrinque rotundatae, 30–36 \times 12–13 μ .

Hab. in foliis *Oldenlandiae decumbentis*, Entebbe Road, *Hansford 1253*.

Differs distinctly from its close relation *M. Mitragynes* in its hyphopodia.

41. *MELIOLA OPPOSITA* H. & P. Syd. in Elmer, Leafl. Philippine Bot. vi, p. 1924 (1913). [3112.3222.]

On *Trichilia* sp., Dummer 3920 (previously referred to *M. Trichiliae* Beeli, which according to Stevens in Ann. Myc. xxvi, p. 230 (1928), is a synonym of the above).

42. *MELIOLA PALMICOLA* Wint. in Hedwigia, xxvi, p. 31 (1887). [3131.5332.]

On *Phoenix reclinata*, Dummer 916; on *Raphia* sp., Bombo Road near Kampala, *Hansford 759*; very common.

43. *MELIOLA PAULLINIAE* Stevens in Illinois Biol. Monogr. II, p. 45 (1916). [3111.3222.]

On *Paullinia pinnata*, Dummer 2509; *Hansford 1285, 1376, 1394*; very common wherever the host occurs.

44. *MELIOLA PHYTOLACCAE* Hansford et Stevens, sp. n. [3133.3221.]

Plagulae epiphyllae, rarius hypophyllae, orbiculares, atrae, 1–4 mm. diam., densae, velutinae. *Mycelium* ex hyphis brunneis plus-minusve undulatis septatis (articulis 12–17 μ longis) alternatim vel irregulariter ramosis 6–8 μ crassis compositum. *Hyphopodia capitata* alternata, rarius opposita, numerosa, 14–19 μ longa, cellula basali 2–5 μ longa, cellula apicali 9–15 μ longa et lata rotundata. *Hyphopodia mucronata* alternata vel opposita, inter hyphopodia capitata interspersa, haud numerosa, ampullacea, collo brevi. *Setae myceliales* numerosissimae, erectae, rectae, atro-brunneae, sub-pellucidae, 180–230 μ longae, basi 7–9 μ crassae, sursum pallidiores, apice dentatae, vel irregulariter

2-3-furcatae. *Perithecia globosa*, 120–160 μ diam., atra, verrucosa, in centro plagularum gregaria. *Asci* bispori. *Sporae* 4-septatae, brunneae, cylindraceae, utrinque late rotundatae, constrictae, 34–39 \times 11–15 μ .

Hab. in foliis *Phytolaccae dodecandrae*, Masaka Road prope Kampala, Uganda, *Hansford 1324*.

The colonies are very dense, semi-crustose, and the hyphae and hyphopodia form almost a solid tissue.

45. **MELIOLA PLANTAGINIS** Hansford et Stevens, sp. n. [3111.3221.]

Plagulae amphigenae, plerumque epiphyllae, atrae, orbiculares, 1–2 mm. diam. *Mycelium* ex hyphis reticulatis brunneis undulatis vel subrectis septatis (articulis 30 μ longis) opposite ramosis 6·5–8 μ crassis compositum. *Hyphopodia capitata* alternata, 16–20 μ longa, cellula basali 4–5 μ longa, cellula apicali rotundata elliptica vel rarius sub-lobata 12–16 μ longa et 10–12 μ lata. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, opposita, ampulliformia. *Setae myceliales* erectae, sub-rectae, atrae, sursum pallidiores 170–280 μ longae, basi 7–8·5 μ crassae, apice obtusae. *Perithecia globosa*, atra, in centro plagularum gregaria, verrucosa, 140–210 μ diam. *Sporae* 4-septatae, atro-brunneae, cylindraceae utrinque rotundatae, leniter constrictae, 30–35 \times 11–12½ μ .

Hab. in foliis *Plantaginis* sp., Mt. Nkokonjeru, *Hansford 796*.

46. **MELIOLA PLUMBAGINIS** Hansford et Stevens, sp. n. [3113.4223.]

Plagulae amphigenae et cauliniae, densae, 1–2 mm. diam., saepe numerosissimae confluentes, maiores irregulares, velutinae. *Mycelium* ex hyphis reticulatis brunneis rectis septatis (articulis 15–20 μ longis) opposite vel irregulariter ramosis 7–9 μ crassis compositum. *Hyphopodia capitata* numerosissima, opposita vel alternata, 12–20 μ longa, cellula basali brevi cylindracea 2–7 μ longa, cellula apicali rotundata vel subangulata 10–14 μ longa et 10–13 μ lata. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, opposita, ampullacea, collo brevi curvato. *Setae myceliales* erectae, numerosissimae, rectae, atrae, opacae, simplices, 300–700 μ longae, basi 11–14 μ crassae, sursum attenuatae, apice acutae. *Perithecia* atra globosa, verrucosa, numerosa, 160–200 μ diam. *Asci* bispori. *Sporae* 4-septatae, brunneae, cylindraceae, utrinque late rotundatae, leniter constrictae, 40–49 \times 13–17 μ .

Hab. in foliis et caulinibus *Plumbaginis* sp., Entebbe Road, Uganda, *Hansford 1457*.

Common on this host in wet places and strongly parasitic, causing defoliation and death of branches.

47. **MELIOLA POLYTRICHA** Kalchbr. & Cooke ex Cooke in Grevillea, viii, p. 72 (1879). [3111.5221.]

On *Pittosporum* sp., Kampala, *Hansford 1987*.

48. MELIOLA PSYCHOTRIAE Earle in Bull.N.Y. Bot. Gard. III, p. 308 (1905). [3111.3221.]

On *Pentas longiflora*, Masaka, Hansford 1556; (?) on *Mimulopsis* sp., Butambala, Hansford 1417.

49. MELIOLA RHOIS P. Henn. in Engl. Bot. Jahrb. XVII, p. 523 (1893). [3111.4132.]

On *Rhus* sp., Entebbe Road, Hansford 1254 (p.p.), 1438, 1750; common.

50. MELIOLA RHOIS P. Henn. var. MINOR Hansford, var. nov. [3111.3221.]

A typo ita differt:—*plagulae* non crustosae, 1–3 mm. diam.; *hypopodii capitati* cellula apicalis subglobosa vel sublobata, 10–14×8–11 μ; *setae myceliales* 150–250 μ longae; *perithecia* 150–180 μ diam.; *sporae* 37–41×14–18 μ.

Hab. in foliis *Rhois* sp., Entebbe Road, Uganda, Hansford 1254 (p.p.).

Occurs mixed with colonies of the typical form on the same leaves.

51. MELIOLA SAKAWENSIS P. Henn. in Hedwigia, XLIII, p. 141 (1904). [3111.3222.]

On *Lantana* spp., Kampala, Hansford 1077, etc.; very common.

52. MELIOLA SANSEVIERIAE Wakefield, sp. n. [3131.5/6321.]

Coloniae epiphyllae vel amphigenae, maculas atras velutinas rotundatas vel ellipsoideas 1–5 mm. diam. efficienes, interdum confluentes, tunc fere totam folii superficiem obtegentes. *Hyphae* obscure brunneae, undulatae, crasse tunicatae, 7–10 μ crassae, cellulis singulis 20–40 μ longis, oppositae vel alternatim ramosae. *Hyphopodia capitata* alternata vel unilateralia, distantes, 25–30 μ longa, cellula superiore ovato-globosa, 15–20×15–18 μ. *Hyphopodia mucronata* plerumque opposita, truncata, 12–20×10–12 μ. *Setae myceliales* numerosae, rigidae, ad 290 μ longae, interdum basi geniculatae, stipite opaco 10–12 μ crasso, superne ramosae, ramulis ad 2–3 numero 10–30 μ longis iterum apice bi- vel tri-dentatis. *Perithecia* sparsa, atra, globosa, in siccо collapsa, 160–190 μ. *Asci* ovati, bispori. *Sporae* 4-septatae, vix constrictae, oblongae, utrinque rotundatae, 45–51×18–22 μ (plerumque 45–50×18–20 μ).

Hab. in foliis *Sansevieriae Dawei*, Kampala, Uganda, Snowden 718, August 1921 (type); Kampala, July 1918, Mailand 305; July 1921, Snowden, Small 577; Kampala, Hansford 1242.

In the coarse mycelium and large hyphopodia the species resembles *M. Tholoniis*, but it differs in the forked setae and smaller spores. It appears to be near *M. varia* Doidge, but the hyphae and setae are broader and the setae less repeatedly forked. It is larger in every part than *M. furcata* Lev., and forms denser colonies.

53. MELIOLA SCOLOPIAE Doidge in Bothalia, II, p. 437 (1929). [2111.5222.]

On *Aberia macrocalyx*, Butambala, Hansford 1370; Jinja Road, Hansford 1389; on *Flacourtie* sp., Mbarara, Snowden, Hansford 1463.

54. MELIOLA SMALLII Hansford et Stevens, sp. n. [3111.31/224.]

Plagulae effusae, hypophyllae, atrae, tenues. *Mycelium* ex hyphis brunneis flexuosis septatis (articulis 30–45 μ longis) irregulariter ramosis anastomosantibus 6 μ crassis compositum. *Hyphopodia capitata* alternata, saepe recurvata, cellula basali 5–10 μ longa, cellula apicali ovata 12–16 μ longa et 8–11 μ lata. *Hyphopodia mucronata* non visa. *Setae myceliales* haud numerosae, praecipue juxta perithecia evolutae, rectae, erectae, brunneae, 500–1100 μ longae, basi 9–10 μ latae, sursum leniter attenuatae, apice obtusae et plus-minusve pellucidae. *Perithecia* atra, globosa, verrucosa, sparsa, 140–160 μ diam. *Sporae* brunneae, cylindraceae, curvulae, utrinque rotundatae, 4-septatae, leniter constrictae, 33–38 \times 9–10 μ .

Hab. in foliis *Rubiacearum* sp. indet., Butambala, Uganda, *Hansford* 1367.

55. MELIOLA SNOWDENII Hansford et Stevens, sp. n. [3111.3221.]

Plagulae 1–2 mm. diam., orbiculares, amphigenae et caulinolae, densae, atrae. *Mycelium* ex hyphis undulatis brunneis irregulariter ramosis anastomosantibus septatis (articulis 12–20 μ longis) 6–7 μ crassis compositum. *Hyphopodia capitata* alternata vel unilateralia, 20–23 μ longa, cellula basali 5–8 μ longa, cellula apicali subglobosa vel ovata 13–16 \times 10–12 μ . *Hyphopodia mucronata* inter hyphopodia capitata interspersa, opposita, unilateralia vel alternata, ampullacea, collo brevi curvato. *Perithecia* globosa, atra, verrucosa, in centro plagularum laxe gregaria, ad 180 μ diam. *Sporae* 4-septatae, cylindraceae, leniter constrictae, brunneae, 29–32 \times 12–14 μ . *Setae myceliales* erectae, rectae, brunneae, usque ad 220 μ longae, basi 8 μ crassae, apice obtusae, numerosae.

Hab. in foliis *Mimusopsidis* sp., Entebbe, *Hansford* 1383 (leg. J. D. Snowden).

56. MELIOLA STENOSPORA Wint. in Hedwigia, xxv, p. 97 (1886). [3111.4222.]

On *Piper* sp., Kipayo, *Dummer* 2168; (?) on *Convolvulaceae*, *Dummer* 618, 2182.

57. MELIOLA STROPHANTHI Hansford, sp. n. [3111.4222.]

Plagulae epiphyllae, orbiculares, 1–2 mm. diam., atrae, densae, crustosae. *Mycelium* ex hyphis atro-brunneis 7–9 μ crassis septatis (articulis 12–16 μ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata, rarissime opposita, 18–28 μ longa, cellula basali cylindracea 4–9 μ longa, cellula apicali ovata rarius sub-lobata 12–20 \times 10–12 μ . *Hyphopodia mucronata* numerosa, praecipue in centro plagularum evoluta, ampullacea, opposita, collo brevi curvato. *Setae myceliales* sparsae vel numerosissimae, atrae, septatae, simplices, rectae, 250–400 \times 9–10 μ , sursum attenuatae, apice acutae. *Perithecia* atra, globosa, verrucosa, sparsa, 140–180 μ diam. *Sporae* cylindrica, utrinque rotundatae, atro-brunneae, 4-septatae, constrictae, 42–46 \times 15–17 μ .

Hab. in foliis *Strophanthi* sp., Masaka Road, *Hansford* 1785.

58. MELIOLA TODDALIAE Hansford, sp. n. [3111.5333.]

Plagulae atrae, orbiculares, epiphyllae, 1–3 mm. diam., densae, velutinae. *Mycelium* ex hyphis atro-brunneis rectiusculis 9–10 μ crassis septatis (articulis

$20-30\ \mu$ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata, clavata, interdum reflexa, $25-30\ \mu$ longa, cellula apicali ovata vel rotundata $19-22 \times 11-14\ \mu$, cellula basali $7-10\ \mu$ longa. *Setae myceliales* numerosae, atrae, erectae, rectae vel leniter curvatae, $450-680\ \mu$ longae, apice acutae, simplices vel breviter 2-dentatae (ad $8\ \mu$). *Perithecia* sparsa, atra, globosa, verrucosa, $200-240\ \mu$ diam. *Asci* 2-spori, fugaces. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, $52-56 \times 19-23\ \mu$.

Hab. in foliis *Toddaliae asiatica*, Kampala, Hansford 1908.

59. *MELIOLA TERAMNI* H. & P. Syd. in Ann. Myc. xv, p. 193 (1917). [311/33. 3223.]

On *Leguminosae* indet., Butambala, Hansford 1420.

60. *MELIOLA THOLLONIS* Gaill. Le Genre Meliola, p. 88 (1892). [3111.6332.]

On an undetermined plant (? *Sterculiaceae* or *Euphorbiaceae*), Dummer 1481. This specimen has been re-examined recently by Miss Wakefield, who confirms the determination of the *Meliola*.

61. *MELIOLA THOMASII* Hansford, sp. n. [3132.4223.]

Plagulae plerumque epiphyllae, atrae, orbiculares, velutinae, densae, $0.5-2$ mm. *Mycelium* ex hyphis atro-brunneis rectis $7-8\ \mu$ crassis septatis (articulis $17-25\ \mu$ longis) opposite ramosis compositum. *Hyphopodia capitata* numerosissima, opposita, $14-18\ \mu$ longa, cellula apicali rotundata vel ovata $8-12 \times 8-10\ \mu$, cellula basali cylindracea $3-7\ \mu$ longa. *Hyphopodia mucronata* non visa. *Setae myceliales* rectae, atrae, opacae, numerosissimae, $350-600\ \mu$ longae, apice acutae, dentatae (ad $15\ \mu$), rarius simplices. *Perithecia* sparsa, atra, globosa, verrucosa, $180-230\ \mu$ diam. *Sporae* late ellipsoideae, atro-brunneae, 4-septatae, constrictae, $39-41 \times 17-19\ \mu$.

Hab. in foliis *Trichiliae* sp., Kyagwe, Hansford 1937.

62. *MELIOLA UGANDENSIS* Hansford, sp. n. [3143.5231.]

Plagulae caulincola, atrae, orbiculares, $1-4$ mm. diam., densae, velutinae. *Mycelium* ex hyphis brunneis rectis septatis (articulis $15-22\ \mu$ longis) opposite ramosis anastomosantibus $7-9\ \mu$ crassis compositum. *Hyphopodia capitata* numerosa, alternata unilateralia vel opposita, recta vel curvula, cellula basali $4-5\ \mu$ longa, cellula apicali $12-15\ \mu$ diam. sub-globosa vel globosa vel ovata. *Hyphopodia mucronata* haud numerosa, inter hyphopodia capitata interspersa, opposita, ampullacea, $16-18 \times 10-12\ \mu$, collo brevi curvato. *Setae myceliales* numerosae, erectae, atrae, opacae $140-220\ \mu$ longae, ad basin $10-12\ \mu$ crassae, ad apicem pellucidae, apice repetitive bi- vel tri-furcatae (ad $50\ \mu$). *Perithecia* sparsa, atra, globosa, verrucosa, $120-240\ \mu$. *Asci* 2-4-spori, fugaces. *Sporae* 4-septatae, brunneae, cylindraceae utrinque late rotundatae, rectae vel curvulae, $46-52 \times 15-18\ \mu$, constrictae.

Hab. in caulis *Euphorbiae* sp., Kampala, Hansford 1104.

63. *MELIOLA VICINA* Syd. in Ann. Myc. xxi, p. 95 (1932). [3111.3212] (for Uganda specimen; type given by Stevens in Ann. Myc. xxvi, p. 235 as 3111. 4222).

On *Craterispermum* sp., Entebbe Road, *Hansford 1441* (det. F. L. Stevens).

64. *MELIOLA VOACANGAE* Hansford et Stevens, sp. n. [311/21.4221.]

Plagulae amphigenae, atrae, orbicularis, 1–3 mm. diam., tenues, numerosae. *Mycelium ex hyphis brunneis undulatis septatis (articulis 12–20 μ longis) opposite ramosis 7–9 μ crassis compositum.* *Hyphopodia capitata numerosa, alternata, 16–25 μ longa, cellula basali 3–9 μ longa, cellula apicali rotundata vel irregulariter sub-lobata 11–17 μ longa et 12–17 μ lata.* *Hyphopodia mucronata numerosa, opposita vel unilateralia, ampullacea, collo brevi curvato.* *Setae myceliales haud numerosae, sparsae vel gregatim (4–8) juxta perithecia dispositae, atro-brunneae, erectae, rectae vel curvatae, 180–230 μ longae, basi 9–10 μ crassae, apice obtusae.* *Perithecia atra, globosa, verruculosa, sparsa, 120–160 μ diam.* *Asci bispori, fugaces.* *Sporae brunneae, 4-septatae, curvulae, leniter constrictae, 38–44 \times 14–18 μ .*

Hab. in foliis *Voacangae* sp., Masaka Road, Uganda, *Hansford 1475 a.*

65. *MELIOLA WEIGELTII* Kunze in Weigelt's Exsicc. no. 137. [311/33.4233.]

On *Rhus* sp., Kazi, near Kampala, *Hansford 1918.*

66. *MELIOLA WOODIANA* Sacc. ex Syd. in Hedwigia, xxxviii, p. 132 (1899). [3111.5222.]

On *Rubiaceae* indet., Kazi, near Kampala, *Hansford 1912.*

67. *MELIOLA WOODIANA* Sacc. var. *ARISTATA* Hansford, var. nov. [3411. 4221.]

A typo ita differt :—*setae myceliales* 240–300 μ longae ; *setae peritheciales* 0–6, rectae, atrae, acutae, simplices, 120–200 μ longae ; *sporae* 46–50 \times 13–16 μ .

Hab. in foliis *Rubiacearum* sp. indet., Kazi, Kampala, Uganda, *Hansford 1912, p.p.*

This occurs mixed with *M. Woodiana* on the same leaves ; and the perithecial setae, which are often absent from some perithecia while they occur on others in the same colony, are the chief difference from the type.

68. *MELIOLA ZOLLINGERI* Beeli, var. *MINOR* Beeli in Bull. Jard. Bot. Bruxelles, vii, p. 100 (1920). [3131.3221.]

On *Desmodium latifolium*, Dummer 2497.

Contributions to the flora of Mauritius.—I. An account of the naturalized flowering plants recorded from Mauritius since the publication of Baker's 'Flora of Mauritius and the Seychelles' (1877). By R. E. VAUGHAN, Ph.D., F.L.S.

[Read 28 October 1937]

MAURITIUS is one of a group of three volcanic islands situated in the South Indian Ocean. It is in latitude 20° S., about 500 miles east of Madagascar. The area of the island is approximately 700 square miles, of which 216 square miles are under sugar-cane. The original vegetation of the island has been very largely destroyed, and replaced by scrubs and thickets of exotic species.

The first attempt at a flora was the 'Hortus Mauritianus' by W. Bojer, published in 1837. Bojer enumerated the exotic and indigenous plants of the island, gave some account of their distribution, and named, but did not describe, a number of new species. His work was based on material gathered by Thouars, Commerson, and Sieber, and on extensive collections and observations made by himself during his long residence in the island.

During the following decades, principally from 1860–65, L. Bouton and P. H. Ayres collected important material, and the latter prepared a 'Flora' of the island in manuscript. This, together with his collections and those of Bouton, was sent to Kew for the compilation of J. G. Baker's 'Flora of Mauritius and the Seychelles', which was published in 1877.

Johnston (1895), during a residence of over three years in the island from 1887 to 1890, made further contributions to our knowledge of the flora. He collected seventy-eight species of flowering plants not recorded in Baker's 'Flora', of which twenty-five were native. He also investigated and described the flora of the islets surrounding the mainland.

Baker's 'Flora', which is the only standard work on the subject, is now inadequate on account of the large number of native and naturalized species which have been discovered during the last sixty years.

An account is given in this paper of the naturalized flowering plants which have been recorded from the island since the publication of Baker's 'Flora' in 1877. The new native species will form the subject of a further communication.

The number of species here recorded is 139. These may be conveniently divided into two groups as follows :—

1. Immigrant species	82
2. Escapes from cultivation which have become naturalized (indicated by an asterisk in the text).....	57

The plants comprising the first group are for the most part fairly common, and have accessible, though in some cases restricted, habitats. It is therefore safe to assume that in the large majority of cases they have not been overlooked by former collectors, but have arrived during the last 60 years. Their present distribution and country of origin is for this reason a matter of some interest.

It is probable that a very large number of seeds from all parts of the world are continually reaching the island. They may be introduced by various means—on clothing of passengers disembarking on the island, with rice from India, in packets of seeds for cultivation, and so on. Some of them have better opportunities for arriving than others, particularly on account of the geographical position of the island. Most of the shipping calling at Mauritius comes from European ports via South and East Africa, and a much smaller proportion from India and the Far East. It might be expected therefore that plants from Europe and Africa would be prevalent among those newly established. A distribution-table of the invading species throws some light on this point. In the following table the first column gives the native country of the species, while the second shows the present range of the species excluding their native country. The third column indicates the native country of those species which have become established in the Mascarenes (including Madagascar), but not elsewhere :—

Distribution of the immigrant species.

	1. Native country of invading species.	2. Additional range attained by invading species.	3. Native country of the 34 species recorded in the first line of column 2.
Mascarene region	34	..
Tropical Asia	21	4	14
Tropical and South Africa	4	3	2
Asia and Africa	3	3	2
Australia	1
Old World Tropics	2	19	..
Tropical America, including West Indies	23	1	10
North temperate regions	24	..	6
Pantropical	4	18	..

The distribution-figures reveal two points of interest : first, the large number of American species and, second, the very small percentage of African species compared with those of Asia. The European immigrants are well represented, but there is a marked predominance of species from America and Asia.

In considering the manner in which the immigrant species have reached the island, a distinction between species which are restricted in range and those which are widely diffused is important. Thus in the case of 23 American

species 12 are now pantropical and may have reached the island from some other country, possibly Africa or Asia. This is well illustrated in the case of *Acanthospermum hispidum* DC., an American species which appeared in S. Africa in 1915 and was found in Mauritius ten years later. Again, *Nicotiana plumbaginifolia* Viv., another American species, has been established in India for many years and has probably been introduced from there into Mauritius. Further, seeds with special devices for dispersal would seem to have a better opportunity of reaching the island and becoming established. Some of the immigrant species have very small seeds, which are rapidly conveyed from place to place, especially those belonging to the Gramineae. Apart from the grasses, however, it is found that, out of 58 species, only 3 have seeds armed with spines, hooks, or similar modifications for distribution as external passengers. These species are *Acanthospermum hispidum* DC., *Emex spinosa* Campd., and *Medicago denticulata* Willd. They are now all widespread, and none is restricted to the Mascarenes alone.

It is evident that among the large number of seeds of foreign species reaching the island only a very small proportion are likely to become naturalized. The ability of a species to survive and become established in the new environment must depend therefore upon the interaction of various complex and closely interwoven factors, some of which may be enumerated as follows :—(1) Macrobiotic seeds, since they may not be able to find a suitable nidus for germination for some time after arrival. (2) A good germinating capacity. (3) Power to compete successfully with other species already established. (4) Ability of the plant to adapt itself to the climatic conditions of the island, which may differ widely from those of its native country. (5) An effective method of seed-dispersal within the island.

Since so little correlation is found between the country of origin of the new species and the trade-routes, it is probable that the initial advantages of having easier access to the island, or of possessing special modifications for seed-distribution, are masked by the absence in the plants' make-up of the factors contributing to successful naturalization.

Short descriptive notes are given with most species except the Cyperaceae and Gramineae, a full account of which will shortly be published elsewhere. Specimens seen by me are indicated by an exclamation mark after the collector's name. The following abbreviations are used :—V=specimens in my herbarium; Herb. Desj.=Herbarium Desjardins, Mauritius Institute, Port Louis. The order of the enumeration is that of Hutchinson's *Families of Flowering Plants* (1926 ; 1934).

I am much indebted to the Director, Royal Botanic Gardens, Kew, and his staff for the determination of a large number of species.

MAGNOLIACEAE.

***MICHELIA CHAMPACA** Linn. Sp. Pl. p. 536 (1753). 'Champac.' A tall tree, with smooth light grey bark. Leaves ovate-lanceolate, acuminate, 18–25 cm. long by 5–8 cm. broad, with large sheathing stipules. Flowers axillary on

short peduncles, 10 cm. diam. ; perianth segments 14-18, yellow, fragrant. Gynophore stalked ; ovaries pubescent.

Herb. Desj. ! Naturalized in the neighbourhood of Curepipe. Native of Indo-Malaya.

LAURACEAE.

**CINNAMOMUM CAMPHORA* (Linn.) T. Nees & Eberm. *Hand. Med. Pharm.* Bot. II, p. 430 (1831). 'Camphrier.' The Camphor Tree. Introduced by Abbé Gallois about 1750, and frequently planted as a shade and timber tree. It is now naturalized in the higher parts of the Island.

**CINNAMOMUM BURMANNI* Blume, *Bijdr.* p. 569 (1826). Leaves opposite or alternate, ovate-lanceolate, shortly petiolate, prominently three-veined, 7-9 cm. long by 2-3 cm. broad, pink when young. Flowers greenish white in terminal and axillary cymes, not exceeding the leaves.

Probably introduced. Common in forests round Butte Chaumont and Midlands. V/349 ! Native of Malaya.

CRUCIFERAE.

CAPSELLA BURSA-PASTORIS Medic. *Pflanzeng.* p. 85 (1792). Basal leaves lanceolate, pinnatifid. Stem-leaves linear-lanceolate, sessile, sagittate. Racemes many-flowered, up to 20 cm. long. Corolla small, white. Fruit a compressed obcordate triangular siliqua 5-7 mm. long, containing many seeds.

Roadside, Plaines Wilhems, Johnston ! Native of North Temperate regions. An occasional weed not confined to any particular locality.

RORIPA MONTANA Small, Fl. S.E. United States, ed. 2, p. 1336 (1913). A small prostrate annual with reddish-green stems and leaves. Radical leaves ovate, pinnatifid in the lower half, 4-5 cm. long. Petals absent. Pod slender, cylindric, not jointed or swollen, 2-3 cm. long.

A frequent weed in gardens and waste places at Curepipe (1,800 feet). V/601 ! Native of SE. Asia, now naturalized in many countries.

CARYOPHYLLACEAE.

SILENE GALlica Linn. Sp. Pl. p. 417 (1753). A hairy annual. Leaves sessile, obovate-lanceolate, 2.5-4 cm. long. Flowers subsessile in terminal secund leafy racemes. Calyx 10-ribbed ; sepals connate ; teeth linear. Petals small, bifid, purple or white, usually with a white margin. Styles 3 : stamens 10. Capsule 7-8 mm. long, shorter than the calyx.

Roadside near Rose Belle. V/212 ! An occasional weed. Native of Europe.

SILENE ARMERIA Linn. Sp. Pl. p. 420 (1753). A glabrous annual. Leaves sessile, oblong, 3-5 cm. long. Flowers in terminal corymbs. Petals red or purple. Capsule 8-10 mm. long, shorter than the calyx.

Curepipe. A garden escape. Johnston ! Naturalized ? Not seen recently. Native of south Europe.

SAGINA APETALA Linn. Mant. II, p. 559 (1771). A low, much-branched, annual, with stems seldom exceeding 6 cm. Leaves minute, linear, 3-4 cm. long. Sepals free, 4-5, exceeding the capsule. Petals very small or absent. Styles 5. Capsule opening by 4-5 valves.

Common at Curepipe on dry banks and garden paths. V/443 ! Native of Europe.

POLYGONACEAE.

EMEX SPINOSA Campd. Rum. 58, t. i, f. i (1819). Stem prostrate, trailing to a distance of 40-60 cm. Leaves long-petioled, oblong-ovate, 6 to 9 cm. long. Flowers in whorled racemes, males above and females below, or sessile in leaf-axils. Female flowers with a turbinate 6-lobed perianth. Fruit 7-8 mm. long, armed with three spines.

Native of Europe and N. Africa. Johnston ! Rare in Mauritius. Naturalized also in S. Africa.

RUMEX CRIPSUS Linn. Sp. Pl. p. 335 (1753). Stem up to 1 metre high, prominently ribbed. Leaves long-petioled, lanceolate-ovate, acute with undulate margins, 10-20 cm. long by 2-5 cm. broad. Inner perianth-segments oblong-ovate, entire, with a prominent callus on mid-rib. Flowers in dense many-flowered whorls forming a large panicle often exceeding 50 cm. long.

Railway embankment near Curepipe. V/369 ! & V/538 ! A common weed in high stations. Europe and Temperate Asia.

BALSAMINACEAE.

IMPATIENS FLACCIDA Arn. in Hook. Comp. Bot. Mag. I, p. 322 (1835). Glabrous fleshy herb, reaching a height of 60-80 cm. with reddish stems. Leaves alternate long-petiolate, ovate-lanceolate, acute, crenate, up to 10 cm. long, with conspicuous lateral veins. Flowers solitary from the axils of the upper leaves ; pedicels as long as the leaves. Spur recurved, slender, 4-5 cm. long. Corolla reddish purple, 3-4 cm. broad. Capsule glabrous, green, succulent.

Forms dense carpets in the woods round Curepipe and the Mare aux Vacoas. V/732 ! Native of India and Ceylon.

LYTHRACEAE.

**CUPHEA IGNEA* A. DC. in Fl. des Serres. ser. I, v, p. 500 (1849). Annual with angular subglabrous stems. Leaves ovate-acuminate, 2-4 cm. long. Flowers solitary on pedicels exceeding the petioles. Calyx-tube bright red with a white ring at the mouth. Petals absent.

Trou aux Cerfs, an escape. V/40 ! Native of Mexico and South America.

COMBRETACEAE.

**QUISQUALIS INDICA* Linn. Sp. Pl. ed. 2, p. 556 (1762). 'Badamier Sauvage,' 'Rangoon Creeper.' A glabrous climber. Leaves opposite, oblong, 9–11 cm. long by 3–4 cm. broad, petiole 2 cm. Calyx-tube deciduous, prolonged 1–1·5 cm. above the ovary. Corolla deep red, with a long tube often exceeding 5 cm. Fruit 5-angled, 3–4 cm. long.

Naturalized in many places. Introduced from India. V/576 !

TERMINALIA ARJUNA W. & A. ex Bedd. Fl. Sylv. t. 28 (1869). A tree with smooth deciduous reddish-grey bark. Leaves oblong-obtuse, glabrous, up to 25 cm. long, suddenly narrowed at the base. Petiole seldom exceeding 1 cm. long with two glands. Flowers in paniculate spikes. Calyx glabrous ; petals absent ; ovary covered with dense brown hairs. Fruit ovoid-oblong, 3–5 cm. long, with five acute truncate wings.

Frequently planted by roadsides as a shade tree. Native of India.

TILIACEAE.

**ELAEOCARPUS SERRATUS* Linn. Sp. Pl. p. 515 (1753). A large tree with smooth grey bark. Leaves obovate-serrate, 5–6 cm. long by 2·5–3 cm. broad. Flowers in short axillary racemes, not exceeding the leaves.

Naturalized round Midlands and Butte Chaumont. V/399 ! Native of Indo-Malaya.

EUPHORBIACEAE.

**ACALYPHA GRANDIS* Benth. in Hook. Journ. Bot. II, p. 232 (1843). 'Feuille Rouge.' A monoecious shrub. Leaves ovate-serrate, long-petioled, usually red on both surfaces or with a red margin on the upper surface.

Planted frequently for hedges throughout the Island. Naturalized in many places. V/511 ! Native of Malaya and the East Indies.

CROTON sp. An erect annual 30–45 cm. high, with stems, petioles, and under surfaces of leaves clothed with stellate hairs. Leaves ovate, serrate, 3–6 cm. long, with two sessile glands at the base. Flowers in monoecious racemes, the males above, a few females below. Male flowers solitary, style trifid with a bipartite stigma. Ovules solitary in each cell.

Common in waste places round Pt. Louis and Pt. aux Sables. Probably a West Indian species. V/610 !

**EUPHORBIA HETEROPHYLLA* Linn. Sp. Pl. p. 453 (1753). An erect fleshy little-branched annual. Leaves serrate, panduriform, very variable, 8–10 cm. long by 3–5 cm. broad, the leaves bracteating the terminal cymes scarlet towards the base. Glands of involucre without a petaloid appendage.

A common weed in drier parts of the Island. Probably an escape from cultivation. V/708 ! Native of Tropical America.

ROSACEAE.

FRAGARIA INDICA Andr. Bot. Rep. t. 479 (1807). Stems trailing, rooting at the nodes. Leaves distant, trifoliate, long-petioled, crenate, 3–4 cm. long. Flowers solitary; pedicel up to 4 cm. long. Epicalyx of five broad obovate crenate segments. Petals 5, yellow. Fruit ovoid, red, 1 cm. broad.

Cane-fields near the Trois Mamelles. Not common. V/214 ! Native of central and south-east Asia.

CAESALPINIACEAE.

CASSIA LAEVIGATA Willd. Enum. Hort. Berol. p. 441 (1809). A low shrub. Leaflets usually six, ovate, acuminate, subsessile, 4–5 cm. long, the terminal pair usually the largest. Glands between the leaflets cylindrical. Flowers in axillary and terminal racemes, crowded towards the end of a long peduncle. Pod glabrous, 8–10 cm. long.

Common in drier parts of the Island. V/63 ! Tropical regions.

CASSIA MIMOSOIDES Linn. Sp. Pl. p. 379 (1753). Stems up to 80 cm. high, pubescent. Leaves 3–6 cm. long. Leaflets 25–50 pairs, linear, 3–5 cm. long. Flowers solitary or paired from the axils of the leaves; pedicels shorter than the leaves. Corolla yellow. Pod flat, pubescent, up to 5 cm. long.

Near the coloured earths, Chamarel. V/396 ! Common in cane-fields up to 1200 ft. Tropics of the Old World.

***CASSIA SIAMEA** Lam. Encycl. I, p. 648 (1785); *C. florida* Vahl, Symb. Bot. III, p. 57 (1794). A tall tree with leaves up to 30 cm. long and without glands. Leaflets 8–10 pairs, oblong, 5–6 cm. long. Panicle large, pyramidal, the yellow flowers clustered at the end of the branchlets. Pod thin, flat, 20–25 cm. long.

Occasionally planted. Naturalized in a few lowland localities. V/765 ! Native of Malaya and the East Indies.

***DEOLONIX REGIA** Raf. Fl. Tellur. II, p. 92 (1836). *Poinciana regia* Bojer ex Curtis' Bot. Mag. t. 2884 (1829). 'Flamboyant.' Established in many places round Pt. Louis and elsewhere up to 1,200 ft. Native of Madagascar.

PAPILIONACEAE.

***CICER ARIETINUM** Linn. Sp. Pl. p. 738 (1753). A shrubby annual. Leaves 3–5 cm. long. Leaflets 10–15, obovate-oblong, toothed in the upper half, 7–8 cm. long. Flowers solitary from the leaf-axils. Pedicel 1·5–3 cm. long.

Roadside near Curepipe. Johnston ! Cultivated throughout the Tropics.

DESMODIUM PALAEACEUM Guill. & Perr. Fl. Seneg. Tent. p. 209 (1830). A low shrub with stems, petioles, and under surfaces of leaves clothed with dense white hairs. Leaves trifoliate; leaflets ovate-lanceolate, acute, with 12–14

pairs of ascending veins. Flowers in globose heads, 1·5–2 cm. diameter, on short peduncles from the axils of the leaves. Corolla red or yellow.

Occasional in drier localities. V/711 ! Native of tropical and South Africa.

FLEMINGIA CONGESTA Roxb. Hort. Beng. p. 56 (1814). A shrub with pubescent stems, petioles, and under surfaces of leaves. Leaves trifoliate; leaflets 3-veined, the terminal one ovate-acute, 8–10 cm. long; the lateral ones equally cuneate. Flowers in dense axillary racemes, not exceeding the petiole of the leaf. Pod 1 cm. long, glandular, pubescent.

Low levels. Not common. V/611 ! Native of India, south-east Asia, and the Philippines.

LATHYRUS APHACA Linn. Sp. Pl. p. 729 (1753). A weak annual, leafless, the leaves replaced by tendrils. Stipules large, leaf-like, sagittate-cordate. Flowers solitary from the axils of the tendrils. Pedicel 3–4 cm. long. Corolla pale yellow. Pod thin, flat, 5–8-seeded.

Small patches in fields near Vacoas Military Camp. Not seen elsewhere. V/329 ! Native of Europe.

LATHYRUS SPHAERICUS Retz. Obs. III, p. 39 (1783). Leaflets two, linear, 5–6 cm. long; tendril unbranched. Flowers usually solitary; pedicel very variable, ½–3 cm. long. Corolla red. Pod thin, 5 cm. long, 10–12-seeded.

Rare. Vacoas Military Camp, not seen elsewhere. V/457 ! Native of Europe and Asia.

MEDICAGO DENTICULATA Willd. Sp. Pl. iv, p. 1414 (1803). Annual, with grooved stems. Leaflets three, obovate-cuneate, 1–2 cm. long. Peduncles 2–6-flowered, not exceeding the leaves. Flowers yellow, 4–5 mm. long. Pod indehiscent, spinous, coiled into 2–3 close spirals, many-seeded.

Common in high stations. Probably spread from Vacoas Military Camp. Johnston ! V/353 ! Native of North Temperate regions of the Old World.

MEDICAGO LUPULINA Linn. Sp. Pl. p. 779 (1753). 'Black Medick.' Stem procumbent. Leaflets three, obovate, faintly toothed or crenate, ½–1 cm. long. Flowers minute, yellow in cylindrical heads; peduncle 15–20-flowered, exceeding the leaves. Pod smooth, minute, reniform, unarmed, one-seeded.

Not common. Johnston ! Native of North Temperate regions.

***MELILLOTUS ALBA** Desv. in Lam. Encycl. IV, p. 63 (1798). Annual or biennial 25–50 cm. high. Leaves trifoliate; petiole 4–5 cm. long. Leaflets toothed, oblong-lanceolate, the terminal one up to 3 cm. long. Racemes terminal and axillary, 5–10 cm. long, many-flowered. Corolla white, the standard exceeding the wings and keel. Pod minute, one-seeded, black when ripe.

Roadside near Souillac. An occasional weed in drier parts of the Island. V/170 ! Native of Europe and Asia.

***PONGAMIA GLABRA** Vent. Jard. Malm. t. 28 (1803). Tall tree. Leaflets 5–7, opposite, ovate-acuminate, 6–10 cm. long. Flowers white or purplish in long-peduncled axillary racemes. Pod flat, woody, with a recurved beak.

Naturalized on the slopes on Mt. Ory and in lowland river reserves. V/1021 ! Native of SE. Asia.

***PTEROCARPUS INDICUS** Willd. Sp. Pl. III, p. 904 (1803). ‘Sang Dragon.’ Leaves imparipinnate. Leaflets alternate, 7–9, ovate, acute, 3–5 cm. long. Flowers large, yellow, in slender paniculate racemes. Stamens diadelphous. Pod thin, indehiscent, orbicular, one-seeded, 3–4 cm. broad, the style at right angles to the stalk.

Naturalized round Pt. Louis and on the slopes of Mt. Ory. Native of Tropical Asia.

MORACEAE.

***ARTOCARPUS COMMUNIS** Forst. Char. Gen. p. 101 (1776). ‘Fruit à Pain.’ The Bread-Fruit tree, a native of the Pacific Islands, is subspontaneous in the vicinity of settlements.

URTICACEAE.

BOEHMERIA MACROPHYLLA D. Don, Prodr. Fl. Nep. p. 60 (1925). Shrub 2–3 cm. high, with stout angular branches. Leaves opposite, lanceolate, 15–25 cm. long by 3–4 cm. broad, serrate, pubescent beneath, prominently 3-ribbed. Spikes 20–30 cm. long, pendulous. Flowers in globose heads 5–7 mm. diameter.

Trou aux Cerfs. V/405 ! Forest-stream near Curepipe. Johnston ! Common in upland woods. Native of Himalaya and Burma.

***PILEA MICROPHYLLA** (Linn.) Liebm. in Vidensk.-Selsk. Skr. 5², p. 302 (1851). Occurs in two forms in Mauritius:—(1) Stem creeping; leaves ovate, minute, 2 mm. long, with flowers and smaller leaves in their axils; petiole as long as the leaves. (2) Stem erect; leaves larger, obovate.

Common everywhere in high stations. Johnston ! Frequently cultivated in the Tropics. Native of Tropical America.

SANTALACEAE.

***SANTALUM ALBUM** Linn. Sp. Pl. p. 349 (1753). ‘Sandalwood.’ Low tree with ovate, opposite, exstipulate leaves, turning black on drying. Flowers small, greenish, in axillary cymose racemes. Calyx 4-lobed, valvate. Petals absent.

Naturalized in many places on the north-west coast. V/737 ! Native of India and Malaya.

RHAMNACEAE.

RHAMNUS NIPALENSIS M. Laws. in Hook. f. Fl. Brit. Ind. I, p. 640 (1875). ‘Liane cerf.’ Leaves alternate, oblong-ovate, acuminate, serrate, 10–12 cm.

long, with 6–8 pairs of ascending lateral veins; petiole 2–3 cm. long. Flowers in short leafy axillary racemes. Petals oblong. Disk thin. Fruit 2–3-lobed, obovoid, indehiscent.

Naturalized in river-gorges near Reduit. Bijoux ! V/617 ! Native of Himalayan regions.

RUTACEAE.

**MURRAYA EXOTICA* Linn. Mant. 2, p. 563 (1771). ‘Bois de buis.’ A much-branched unarmed aromatic shrub. Leaflets 7–9, alternate, oblique, glaucous, obovate-oblong, 1½–2 cm. long. Corolla white, fragrant. Petals imbricate. Stamens 10, unequal; filaments linear. Style long; stigma capitate. Ovary 2-celled. Fruit the size of a large pea, 1–2-seeded.

Naturalized near Case Noyale and Chamarel. V/346 ! Native of Tropical Asia and Australia.

ANACARDIACEAE.

**SCHINUS TEREBINTHIFOLIUS* Raddi in Mem. Med. xvii, p. 399 (1820). ‘Poivre marron.’ A much-branched balsamiferous low tree. Leaves compound, the petiole winged in the upper half; leaflets 4–6, obscurely serrate, ovate-lanceolate, 5–7 cm. long, the terminal the largest. Flowers greenish white, in dense terminal and axillary panicles. Fruit red, the size of a small pea.

On the Trou aux Cerfs and in forests at Midlands. V/607 ! Native of Tropical America.

UMBELLIFERAE.

APIUM LEPTOPHYLLUM F. Muell. ex Benth. Fl. Austral. III, p. 372 (1866). A slender erect annual with smooth terete stems. Leaves 2–3 cm. long, cut to the base into capillary segments. Umbels simple, leaf-opposed, 2–3 from the same node; peduncle 1–2 cm. long, 8–10 rayed pedicels 2–5 mm. Corolla minute, white. Mericarps prominently 5-ribbed with one vitta in each furrow.

Common weed round Curepipe and Vacoas. V/331 ! Native of Australia.

SAPOTACEAE.

**MIMUSOPS BOJERI* DC. Prodr. VIII, p. 265 (1844). ‘Pomme jacot.’ A much branched low tree. Leaves opposite or whorled, rigidly coriaceous, dark green, oblong-ovate, sometimes emarginate, 10–12 cm. long by 6–8 cm. broad. Flowers solitary or fascicled from the upper leaf-axils. Fruit depressed-globose, 2½–3 cm. diam.; peduncle 8–10 cm. long.

Established in many places round the coast. V/701 ! Native of Madagascar.

MYRSINACEAE.

**ARDISIA CRENATA* Roxb. Hort. Beng. p. 85 (1814). An erect undershrub, 40–80 cm. high. Leaves shortly petioled, ovate-lanceolate, 8–10 cm. long by

3–4 cm. broad, with undulate glandular margins. Flowers in terminal and lateral, usually simple umbels; peduncle 8–10 cm. long. Corolla white, with pink glandular dots. Stamens free; style long, not persisting in fruit. Berry red, glossy.

Extremely common on the hills, penetrating into the dense forests. V/718 ! A variety with white berries may be found in neighbourhood of Grand Bassin. Native of India and south-east Asia.

**ARDISIA HUMILIS* Vahl, Symb. Bot. III, p. 40 (1794). A low shrub. Leaves obovate-lanceolate, 5–8 cm. long by 2–3 cm. broad, shortly petioled. Corolla violet with gland-dotted petals, 7–8 mm. long by 4 mm. broad. Style simple, 8 mm. long, projecting beyond the connate anthers. Berry globose, deep blue or black.

Nouvelle Decouverte and Curepipe. Not common. V/504 ! Native of Malaya.

OLEACEAE.

**LIGUSTRUM WALKERI* Dcne. in Nouv. Arch. Mus. Par. ser. 2, II, p. 27 (1879). A much-branched shrub with grey terete branchlets. Leaves opposite, shortly petioled, ovate, 4–6 cm. long. Flowers in copious, much-branched, deltoid panicles. Calyx minute, truncate. Corolla-segments 4, white, valvate, fragrant, 2 mm. long. Fruit purple, oblong or globose.

Frequently planted for hedges and as cover for conifers. It is established everywhere, and is now a conspicuous feature of the upland vegetation. In many places it forms pure stands and is replacing the indigenous flora. V/583 ! Native of Ceylon.

**NORONHIA EMARGINATA* Thou. Gen. Nov. Madag. p. 8 (1811). A low much-branched tree, with smooth grey terete branches. Leaves opposite, obovate, emarginate, rigidly coriaceous, the veins scarcely visible on the under surface; blade 12–14 cm. long by 6–7 cm. broad. Petiole channelled, swollen, 1 cm. long. Racemes short, few-flowered. Fruit smooth, ovoid, 1–2 cm. long.

Established in many places round the coast. V/676 ! A native of Madagascar.

ASCLEPIADACEAE.

CYNANCHUM CALLIALATA Buch.-Ham. ex Wight, Contrib. Bot. Ind. p. 56 (1834). Climber. Leaves opposite, distant, ovate, acuminate, 6–8 cm. long by 4–5 cm. broad, with 8–10 pairs of lateral veins. Cymes shortly peduncled, not exceeding the petioles. Flowers 1 cm. diam., glabrous; corona cupular, irregularly 5-lobed, crenate. Staminal column very short. Follicles 6–8 cm. long, dorsally compressed.

Scrub near estuary of the Grande Rivière Nord-Ouest. Common in low levels. V/545 ! Native of India.

RUBIACEAE.

**MORINDA CITRIFOLIA* Linn. Sp. Pl. p. 176 (1753); Baker, Fl. Maurit. p. 153 (1877). 'Bois tortue.' A low tree with large glossy ovate leaves and quadrangular branchlets. Flowers in dense fused peduncled axillary and terminal heads. Fruits pale yellow, ovoid, 6-8 cm. long.

Common near the sea, particularly on the west coast. Indo-Malaya to the Pacific Islands.

COMPOSITAE.

ACANTHOSPERMUM HISPIDUM DC. Prodr. v, p. 522 (1836). 'Upright Star Burr.' An erect, densely hairy annual. Leaves very variable in shape and size, ovate-oblong, with undulate obscurely serrate margins. Flowers in axillary heads. Achene armed with hooked spines, with two spreading hooked spines at the apex, 5 mm. long.

Frequent in the vicinity of Pt. Louis and Pamplemousses. V/557 ! Probably introduced into Mauritius from South Africa, where it was first found in 1915. Native of tropical America.

AMBROSIA ARTEMISIIFOLIA Linn. Sp. Pl. p. 988 (1753). Annual, pubescent, leaves deeply pinnatisect. Male flowers yellow, arranged in drooping slender terminal racemes with a green cup-shaped involucre. Female flowers solitary or clustered in the leaf-axils.

A common roadside weed round Rose Hill, Réduit, and Quatre Bornes. V/438 ! Native of North America.

ARTEMISIA VULGARIS Linn. Sp. Pl. p. 848 (1753). Perennial. Lower leaves pinnately 3-5-lobed, 5-7 cm. long, dark green above, white below; upper leaves linear-lanceolate. Inflorescence a many-flowered panicle. Heads few-flowered, orange or brown, 3-5 mm. diam. Anthers not tailed at the base. Pappus 0. Involucral bracts biseriate.

A common weed in higher parts of the Island. V/593 ! Native of Europe.

**BOLTONIA INDICA* Benth. Fl. Hongk. p. 173 (1861). Annual, with obovate-lanceolate leaves. Heads on leafy peduncles. Ray-flowers blue.

Roadside at Curepipe and Vacoas. Johnston ! An escape from cultivation. Native of Malaya and China.

DICROCEPHALA BICOLOR Schlecht. in Linnaea, xxv, p. 209 (1833). Annual. Stems 30-50 cm. high, pubescent towards the top. Leaves ovate, inciso-crenate; lower leaves pinnatisect, 5-6 cm. long by 3 cm. broad; petiole 1-2 cm. long. Heads few, paniculate, globose, 3-4 mm. diam. Flowers all perfect, tubular, greenish grey. Pappus absent.

A common weed round Curepipe and Vacoas. Johnston ! Tropical Africa and Asia.

ERIGERON CANADENSE Linn. Sp. Pl. p. 863 (1753). An erect hairy annual, 50 cm.-1 m. high. Leaves sessile, lanceolate, up to 5 cm. long, the lower

ones usually toothed. Flower-heads small, forming a large leafy panicle. Ray-florets linear, not exceeding the acuminate involucral bracts; tubular florets pale yellow or white.

One of the commonest weeds in higher parts of the Island. Johnston ! V/597 ! A cosmopolitan weed.

**ERIGERON MUCRONATUM* DC. Prodr. v. p. 285 (1836). 'Petit lastron,' 'Marguerite marron.' A prostrate wide-spreading perennial with alternate leaves. Upper leaves ovate-lanceolate, entire; lower 3-5-lobed. Heads usually solitary on long peduncles. Ray-florets white or pink.

Very common on walls and banks round Vacoas and Curepipe. V/50 ! Native of tropical America.

MIKANIA SCANDENS Willd. Sp. Pl. III, p. 1743 (1804). A climber, with glabrous stems. Leaves opposite, long-petioled, ovate, acuminate, 6-7 cm. long by 3-4 cm. broad. Heads few-flowered, arranged in globose corymbose clusters. Flowers pale yellow or white, all tubular, hermaphrodite. Anthers rounded at the base, not tailed. Pappus with numerous setae.

Near tea-plantation, Curepipe. V/507 ! Native of tropical America. Now naturalized in many countries.

TARAXACUM OFFICINALE Weber in Wigg. Prim. Fl. Holsat. p. 56 (1780). The European 'Dandelion.' Common everywhere.

LOBELIACEAE.

ISOTOMA LONGIFLORA Presl, Prodr. Lobel. p. 42 (1836). 'Lastron.' Annual, with fleshy stems 30-40 cm. high. Leaves linear-lanceolate, dentate, with spinous margins, decurrent, 12-14 cm. long. Flowers solitary from the axils of the leaves. Corolla white; tube up to 10 cm. long. Calyx 10-ribbed, the five segments produced into linear spinous teeth. Capsule pendulous, dehiscing by apical pores.

A common weed in higher parts of the Island. Poisonous. V/79 ! Native of tropical America.

BORAGINACEAE.

CORDIA INTERRUPTA DC. Prodr. IX, p. 491 (1845). 'Herbe Condé.' A low, much-branched shrub. Leaves ovate-lanceolate, serrate, pubescent beneath, gland-dotted above, shortly petioled, 7-10 cm. long by 2-3 cm. broad. Calyx-segments 5, deltoid. Corolla white; style twice forked. Drupe red, globose, 3-5 mm. diam.

Established everywhere round the coast and in low levels generally. V/478 ! The food-plant of *Typhia parallela*, the parasite of the sugar-cane root beetle *Phytalis smithi* Arrow. Native of tropical America.

SOLANACEAE.

NICOTIANA PLUMBAGINIFOLIA Viv. Elench. Pl. Hort. Dinegro, p. 26, t. 15 (1802). A tall growing annual with glandular pubescent stems and leaves, 30 cm.-1 m. high. Basal leaves ovate-oblong, 10-15 cm. long, with undulate margins; stem-leaves small, linear. Calyx 10-ribbed. Corolla pale purple, 2-3 cm. long.

Established round Pt. Louis. V/370 ! Native of tropical America. Naturalized in India.

CONVOLVULACEAE.

***PORANA PANICULATA** Roxb. Hort. Beng. p. 13 (1814). A climber, with tomentose stems. Leaves petioled, alternate, ovate-cordate, 6-8 cm. long by 5-6 cm. broad. Panicles very numerous from the axils of the leaves. Calyx minute, tomentose. Corolla white; tube 2-3 mm. long.

Sometimes found near Cassis and Coromandel, probably in abandoned gardens. V/736 ! Native of south-east Asia.

CUSCUTA REFLEXA Roxb. Pl. Corom. p. 23, t. 104 (1798). Stems pale yellow-green, 2-3 mm. diam. Racemes dense, few-flowered. Corolla white, urceolate, 5-7 mm. long, with very short reflexed deltoid lobes. Scales shortly fimbriate. Stamens inserted at the top of corolla-tube; filaments very short or wanting. Stigmas two, stout, sessile.

On shrubs at Moka. Johnston ! Common everywhere in higher parts of the Island. V/19 ! Native of south-east Asia.

CUSCUTA CHINENSIS Lam. Encycl. II, p. 229 (1786). Stems slender, reddish yellow, 1-2 mm. diam. Corolla pale yellow, campanulate, 2-3 mm. long, the ovate obtuse lobes as long as the tube. Scales broad, fimbriate. Stamens with filaments exceeding the corolla-lobes. Styles 2 mm. long. Stigmas capitate.

Rose Belle, parasite on *Acalypha grandis* Benth. V/875 ! Not common. Tropical regions of the Old World.

SCROPHULARIACEAE.

***ANTIRRHINUM ORONTIUM** Linn. Sp. Pl. p. 617 (1753). Annual. Stems up to 50 cm. high, glabrous towards the base, pubescent above. Leaves linear, 3-5 cm. long. Flowers axillary; pedicel very short. Calyx-segments narrow, exceeding the corolla. Corolla 1½-2½ cm. long, red or purple.

Cane-fields, Plaines Wilhelms. Johnston ! An escape. Native of Europe and temperate Asia.

CALCEOLARIA MEXICANA Benth. Pl. Hartw. p. 47 (1839). Annual, 20-30 cm. high. Stems and leaves clothed with soft white glandular hairs. Leaves ovate, inciso-crenate, the lower ones pinnatifid. Racemes leafy, few-flowered; pedicel 2-3 cm. long. Calyx-segments 5, free to the base. Corolla pale yellow, with a recurved inflated lower lip.

Roadsides and waste places round Curepipe and Vacoas. V/189 ! Native of Mexico.

LINARIA CYMBALARIA Mill. Gard. Dict. ed. 8, no. 17 (1768). 'Toad flax.' Trailing perennial, with long-petioled, round, lobed leaves and solitary long-pedicelled flowers.

A pest in lawns at Vacoas, Rose Hill, and uplands generally. V/359 ! V/963 ! Native of Europe.

STEMODIA PARVIFLORA Ait. Hort. Kew. ed. 2, iv, p. 52 (1812). A hispid annual, with trailing or suberect stems. Leaves opposite, ovate, petioled, serrate in the upper half, 0·5-2 cm. long. Flowers 1-3 in the leaf-axils. Calyx-segments 5, linear, one-nerved, free to the base. Corolla pale blue, purple, or white; stamens 4, perfect. Capsule compressed, shorter than the calyx.

A common weed at all altitudes. V/498 ! Native of tropical America.

OROBANCHACEAE.

OROBANCHE MINOR Sutt. in Trans. Linn. Soc. Lond. iv, p. 179 (1798). 'Broomrape.' A parasitic herb, the leaves reduced to brown scales. Stem 20-30 cm. Spike many-flowered, the bracts equalling the flowers. Corolla yellow or purplish, 10-15 mm. long.

Parasitic on sweet peas in gardens at Vacoas and Réduit. V/1233 ! Native of Europe and N. Africa.

BIGNONIACEAE.

***TECOMA STANS** Juss. Gen. p. 139 (1789). A much-branched shrub with corky branches. Leaflets 5-7, lanceolate, serrate, 4-5 cm. long. Calyx-teeth short. Corolla yellow, contracted above the base, 4-5 cm. long. Anthers pubescent. Pod linear, 10 cm. long.

Naturalized in many places round the coast. V/491 ! Native of Mexico and the West Indies.

ACANTHACEAE.

ASYSTASIA GANGGETICA T. Anders. in Thwaites, Enum. Pl. Zeyl. p. 235 (1860); Baker, Fl. Maurit. p. 247 (1877). Common everywhere. V/62 ! Very variable, the type usually found at Curepipe, growing in bamboo hedges, has smaller, light green leaves and a much larger corolla. Old World Tropics.

STROBILANTHES COLORATUS T. Anders. in Journ. Linn. Soc. Lond. ix, p. 481 (1867). Stems terete. Leaves opposite, ovate, unequally cuneate at the base, 15 cm. long by 5 cm. broad, serrate, with 6-7 pairs of conspicuous lateral veins. Flowers in copious terminal and axillary cymose panicles. Corolla red or purple.

Naturalized in pine woods near Curepipe. V/417 ! Native of central Asia.

STROBILANTHES ISOPHYLLUS T. Anders. in Journ. Linn. Soc. Lond. ix, p. 478 (1867). Stems tetragonal, with swollen purple nodes. Leaves alternate, ovate, lanceolate, obscurely serrate, subsessile, 5–6 cm. long by 1–1·5 cm. broad, with 3–4 pairs of conspicuous ascending lateral veins. Corolla pale blue with a yellow eye.

Woods and scrub-land near Forest Side. V/512 ! Native of India.

VERBENACEAE.

***DURANTA REPENS** Linn. Sp. Pl. p. 637 (1753). A glabrous, much-branched shrub. Leaves opposite, ovate, serrate, 7 cm. long by 2–3 cm. broad. Flowers in dense terminal and lateral secund racemes. Corolla lilac, 8–10 mm. long. Drupes yellow, the size of a small pea.

Frequently planted for hedges. Now naturalized in woods near Curepipe and the Mare aux Vacoas. V/33 ! Native of tropical America.

***STACHYTARPHETA MUTABILIS** Vahl, Enum. I, p. 208 (1815). Baker, Fl. Maurit. p. 251 (1877). Stems stout, quadrangular, up to 80 cm. high. Leaves pubescent, shortly petioled, ovate, serrate, 7–8 cm. long by 3–5 cm. broad. Spikes stout, cylindrical, 20–30 cm. long with awned bract-leaves. Flowers sessile, rose-red, inserted in hollows of the rachis.

Common at Midlands and Nouvelle France. V/658 ! Native of tropical America.

VERBENA OFFICINALIS Linn. Sp. Pl. p. 20 (1753). An erect hispid annual, with square stems. Leaves ovate, serrate, rugose, the lower pinnatifid or tripartite, 6–10 cm. long. Flowers numerous in long rigid paniculate spikes. Stamens 4, didynamous. Ovary 4-celled, with a single ovule in each cell. Fruit dry, splitting into 4 pyrenes.

A frequent weed at all altitudes. V/26 ! Native of North Temperate regions.

LABIATAE.

HYPTIS FLORIBUNDA Briq. ex Micheli in Mém. Soc. Phys. Hist. Nat. Genève, xxxii, 10, 18, t. 58 (1897). A tall perennial, with woody stems quadrangular below and armed with minute spines above. Leaves ovate, serrate, 2–3 cm. long; petiole $\frac{1}{2}$ – $\frac{2}{3}$ as long as the leaves. Racemes copious, much branched, often exceeding 40 cm. Flowers minute, on very slender pedicels, 2–3 cm. long. Corolla pale purple.

Frequent by roadsides in the vicinity of Vacoas and Curepipe. V/356 ! Native of Paraguay.

OIMUM SANCTUM Linn. Mant. I, p. 85 (1767). Stems short, woody, terete, somewhat pilose. Leaves ovate, serrate, up to 2·5 cm. long. Racemes terminal and axillary, hairy, tetragonal; the flowers 5–6 in a whorl. Calyx deflexed, with a broad ovate upper segment; the two lowest teeth long-awned. Stamens 4, perfect.

Flat Island and Souillac. Common round the coast. V/314 ! South-east Asia to Australia.

STACHYS ARVENSIS Linn. Sp. Pl. ed. 2, p. 814 (1765). A slender annual with much-branched tetragonal hairy stems, up to 30 cm. high. Leaves ovate, petioled, 1·5–2·5 cm. long. Calyx 5-toothed, the teeth exceeding the tube. Corolla pale purple or white, very small. Stamens 4, with glabrous anthers. Whorls 5–7-flowered, subsessile.

Vacoas Military Camp. V/7 ! Native of Europe.

APONOGETONACEAE.

APONOGETON FENESTRALIS Hook. f. in Benth. & Hook. Gen. Pl. III, p. 1014 (1853). A submerged aquatic perennial with a tuberose stem-base. Leaves submerged, perforate, oblong, 20–25 cm. long by 4–6 cm. broad, 12–15-veined. Scape 50–75 cm. long, bifid ; spikes 10–15 cm. long, densely flowered. Flowers hermaphrodite ; perianth segments 3 ; stamens 5–6, unequal. Carpels usually 4.

Watercress-beds at Le Val. V/735 ! Native of Madagascar.

ZINGIBERACEAE.

***HEDYCHIUM CORONARIUM** Koenig in Retz. Obs. III, p. 73 (1783). ‘Longouze. Stems 1–2 m. high. Leaves oblong-lanceolate, 30–50 cm. long by 8–10 cm. broad ; under surface slightly pubescent. Spikes densely flowered. Bract-leaves obovate ; calyx-tube shorter than the bract. Corolla-segments linear, 4 cm. long ; staminodes 5 cm. by 3 cm. Lip bifid, 5 cm. broad, white with a pale green centre. Flowers fragrant.

Common on the hills and in scrub near Curepipe and Midlands. A variety with narrower lip and pale yellow flowers is more common than the type. Native of East Indies.

LILIACEAE.

***GLORIOSA SUPERBA** Linn. Sp. Pl. p. 305 (1753). A climber, with tendril-like leaf-tips. Leaves ovate-lanceolate. Flowers on long pedicels from the axils of the upper leaves. Perianth-segments linear, with undulate margins, yellow-red, 5–7 cm. long. Style 4–5 cm. long, deflexed near the base.

Common on hedges in the neighbourhood of Grand Port. An escape. V/85 ! Native of tropical Asia and Africa.

PONTEDERIACEAE.

***EICHORNIA SPECIOSA** Kunth, Enum. Pl. IV, p. 131 (1843). ‘Water hyacinth.’ Floating aquatic herb. Leaves rhomboid-orbicular, the petiole distended with spongy tissue. Corolla-segments six, blue, the uppermost larger with a bright yellow spot.

Common in streams at Midlands and Cluny, and becoming a pest in certain localities. Native of tropical America, now naturalized in many countries.

IRIDACEAE.

CROCOSMA AUREA Planch. in Fl. des Serres, ser. 1, VII, p. 161 (1851). Corm globose ; stems ancipitous, ribbed. Leaves distichous, up to 50 cm. long. Inflorescence a paniculate spike, the branchlets often flexuose. Perianth deep orange-red ; tube 3-4 cm. long. Segments 2-3 cm. long, spreading. Style-branches simple. Capsule few-seeded, inflated.

Common in fields and scrub-land in high stations. V/81 ! Native of South Africa.

SISYRINCHIUM CHILENSE Hook. Bot. Mag. t. 2786 (1827). Roots fibrous ; stem winged ; lower leaves distichous. Leaves linear, 10-15 cm. long by 4-5 cm. broad. Flowers very small, blue or white, with a yellow throat. Capsule globose, scarcely exceeding 3 mm. diam.

Common weed in lawns and grassy places round Curepipe and Vacoas. V/368 ! Native of tropical America.

TRIMEZA LURIDA Salisb. in Trans. Hort. Soc. I, p. 308 (1812). Corm ovoid ; stems ancipitous ; leaves 30-50 cm. long by 0.5-1 cm. broad. Flowers 3-4 together on a common peduncle, often exceeding 15 cm. Perianth yellow.

Very common in woods and scrub round Curepipe and Midlands. Johnston ! V/295 ! Native of Mexico.

PALMAE.

***RAPHIA RUFFIA** Mart. Hist. Nat. Palm. III, p. 217 (1850). Native of Madagascar. Naturalized by stream banks and marshy places round the Mare aux Vacoas and Midlands.

***Cocos NUCIFERA** Linn. Sp. Pl. p. 1188 (1753). The coconut palm. Frequently cultivated. Established in many places round the coast.

***LIVISTONA CHINENSIS** R. Br. Prodr. p. 268 (1810). A hermaphrodite fan-palm of medium height with pale green leaves, 1 m. diam. Fruit dark purple, the size of a date.

Frequently cultivated in gardens and now naturalized in upland forests. The fruits are distributed by birds. Native of China.

JUNCACEAE.

JUNCUS BUFONIUS Linn. Sp. Pl. p. 466 (1753). Stems densely tufted, 15-25 cm. high. Leaves linear, light green, rarely exceeding the stem. Flowers single in many-flowered paniculate often secund spikes.

Occasional at Vacoas and Curepipe. V/684 ! Native of North Temperate regions.

CYPERACEAE.

FIMBRISTYLIS COMPLANATA Link, Hort. Berol. I, p. 292 (1827). Marshy river-side near sea. Grande Rivière Nord-Ouest. Johnston ! V.B/25 ! All warm countries.

FIMBRISTYLIS QUINQUANGULARIS Kunth, Enum. Pl. II, p. 229 (1837). Bouton ! Nos. 2 & 8. Native of SE. Asia, now naturalized throughout the tropics.

KYLLINGA ODORATA Vahl, Enum. Pl. II, p. 382 (1806). Very common in high stations. Grey ! V.B/71 ! Also tropical Africa, India, and Australia.

KYLLINGA ERECTA Schum. & Thonn. Beskr. Guin. Pl. p. 42 (1827). Grey ! 1858. V.B/73 ! Native of south and tropical Africa.

KYLLINGA EXIGUA Boeck. in Bremen, Abh. VII, p. 36 (1880), *forma explicata* C. B. Cl.

Waste ground at Curepipe. Johnston ! Very common in lawns and meadows at Curepipe and Vacoas. V.B/70 ! Native of Madagascar.

QUEENSLANDIELLA HYALINA (Vahl) Ballard in Hook. Ic. Pl. t. 3208 (1933). Growing in sandy track leading to Pt. aux Sables. V.B/46 ! Very rare. The genus is closely allied to *Kyllinga*, from which it differs in its umbellate inflorescence and 4-5-flowered spikelets. Native of India, introduced into tropical Africa, Australia, and Malaya.

SCLERIA HIRTELLA Swartz, Prodr. p. 19 (1788). Path near Butte Chaumont. Rare in Mauritius. V.B/54 ! Also S. and tropical Africa, Madagascar, and Central America.

GRAMINEAE.

AIRA CAPILLARIS Host, Gram. IV, p. 20, t.35 (1809). Curepipe, not common. Johnston ! Europe.

BOTHRIOCLOA GLABRA (Roxb.) A. Camus in Ann. Soc. Linn. Lyon, LXXVI, p. 162 (1931). Common in scrubland round the coast, V.A/99 ! Madagascar and Old World tropics generally.

***BAMBUSA MULTIPLEX** Rausch, Nomencl. Bot. ed. 3, p. 103 (1797). Frequently planted for hedges throughout the Island and now naturalized in many places, V.A/110 ! Native of China and Japan, cultivated extensively in the tropics.

***DENDROCALAMUS GIGANTEUS** Munro in Trans. Linn. Soc. Lond. XXVI, p. 150 (1868). Cultivated and naturalized in many districts, particularly lowland river reserves. V.A/127 !

DICHANTHIUM ANNULATUM Stapf in Prain, Fl. Trop. Afr. IX, p. 178 (1917). Roadside near Mahebourg. Not common. V.A/100 ! Native of tropical Asia and Africa.

DICHANTHIUM CARICOSUM A. Camus in Lecomte, Fl. Gén. Indochine, VII, p. 318 (1922). Near the Trois Mamelles. V.A/106 ! India, Andaman Islands, and Burma.

DIGITARIA BARBATA Willd. Enum. Hort. Berol. p. 91 (1809). Canefields and paths near Bassin Mill. Also Flat Island. An occasional cane-field weed. V.A/93 ! Native of Java and Indo-China.

ERAGROSTIS PEREGRINA Wiegand in Rhodora, XIX, p. 95 (1917). Curepipe, V.A/33 ! An occasional weed. Probably native in E. Asia, introduced into Europe, N. America, and Australia.

ERAGROSTIS TENUIFOLIA Hochst. ex Steud. Syn. Pl. Glum. I, p. 268 (1854). Near Quatre Bornes, V.A/84 ! Common in low stations. Tropical east Africa and S. India.

ERAGROSTIS UNILOIDES Nees ex Steud. Syn. Pl. Glum. I, p. 264 (1854). Marshy stream-bank near Piton de Milieu. V.A/62 ! Native of tropical Asia, introduced into Africa, America, and Australia.

HEMARTHRIA ALTISSIMA (Poir.) Stapf & C. E. Hubbard in Kew Bull. 1934, p. 109. Abandoned cane-fields at Curepipe. Johnston ! Common round the Mare aux Vacoas and in pine-woods near Curepipe, V.A/60 ! Common in nearly all warm countries.

***IMPERATA CYLINDRICA** Beauv. var. KOENIGII Dur. & Schinz, Consp. Fl. Afr. p. 693 (1898). Grassy banks at Curepipe and at the Mare aux Vacoas, V.A/111 ! Native of tropical Africa, now introduced into most warm countries.

***ISCHAEMUM ARISTATUM** Linn. Sp. Pl. p. 1049 (1753). 'Herbe d'Argent.' Common in upland shrub and grassland. V.A/42 ! Native of India, Indo-Malaya, and China.

PANICUM BREVIFOLIUM Linn. Sp. Pl. p. 59 (1753). Woods near the Mare aux Vacoas. V.A/87 ! Also Seychelles, Indo-Malaya, and China.

PANICUM PALUDOSUM Roxb. Fl. Ind. I, p. 310 (1832). Rare, a few specimens found growing in mud near the Mare aux Vacoas. V.A/14 ! Pantropical.

PASPALUM CONJUGATUM Berg. in Act. Helvet. VII, p. 129 (1772). 'Herbe créole.' Forest at Curepipe, Johnston ! V.A/4 ! Forms an important constituent of the greensward in the pine-woods round Curepipe and elsewhere, frequently replacing other species. A plant of tropical America and the West Indies, now established everywhere in the tropical and sub-tropical regions of the Old World.

PASPALUM DILATATUM Poir. in Lam. Encycl. v, p. 35 (1804). Johnston ! A common weed in gardens and cane-fields. Native of tropical America.

PASPALUM PANICULATUM Linn. Syst. ed. 10, p. 855 (1759). Koenig ! V.A/6 ! Common everywhere in waste places and by roadsides, flowering Dec. to May. Tropical America and West Indies, now introduced into tropical Africa, Mascarene Islands, and other parts of the Old World.

PHALARIS ANGUSTA Nees ex Trin. Gram. Icon. I, t. 78 (1827). Waste ground near Pamplemousses, V.A/124 ! Low levels, but not common. Native of America.

PHALARIS ARUNDINACEA Linn. Sp. Pl. p. 55 (1753). Waste ground near Pamplemousses, V.A/123 ! North Temperate regions and S. Africa.

***POGONATHERUM PANICEUM** Hack. in Allg. Bot. Zeitschr. XII, p. 178 (1906). Introduced into Mauritius from India as an ornamental plant about 1910. V.A/101 ! Now established round Curepipe. Native of India, China, and Malaya.

POLYPOGON MONSPELIENSIS Desf. Fl. Atlant. I, p. 66 (1798). Occasional weed in Black River and Pt. Louis, V.A/138 ! Mediterranean. Naturalized in most warm countries.

***RHYNCHELYTRUM REPENS** (Willd.) C. E. Hubbard in Kew Bull. 1934, p. 110. 'Natal Red-Top Grass.' Introduced as an ornamental grass, now established everywhere round Pt. Louis, Rose Hill, and low levels generally, V.A/28 ! Native of tropical and S. Africa.

SETARIA INTERMEDIA Roem. & Schult. Syst. II, p. 489 (1817). Roadside at Curepipe. Johnston ! Cane-fields and hedges at all altitudes. V.A/38 ! Common in all warm countries.

SETARIA MACROSTACHYA H. B. K. Gen. et Sp. I, p. 110 (1815) ? Occasional weed in the neighbourhood of Flacq and Grandport, V.A/128 ! Native of Asia and Australia.

SETARIA PALLIDE-FUSCA (Schumach.) Stapf & C. E. Hubbard in Kew Bull. 1930, p. 259. A common weed at all altitudes, V.A/23 ! Pantropical.

SETARIA CHEVALIERI Stapf ex Stapf & C. E. Hubbard in Prain, Fl. Trop. Afr. IX, p. 842 (1930). In bamboo hedges at Curepipe, often attaining a height of 6-8 ft. Perhaps introduced as an ornamental grass. V.A/57 ! Native of tropical and South Africa.

SETARIA VERTICILLATA Beauv. Agrost. p. 57 (1812). An occasional weed in cane-fields and cultivated ground. V.A/49 ! 79 ! Pantropical.

TRAGUS BIFLORUS (Roxb.) Schultz, Mant. II, p. 205 (1824). Common in drier parts of the Island. V.A/116 ! Native of India.

VULPIA BROMOIDES S. F. Gray, Nat. Arr. Brit. Pl. II, p. 124 (1821). Railway cutting near Floreal, V.A/115 ! Not common, probably a recent introduction. Native of Europe, naturalized in tropical Africa.

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- (1) BOJER, W. 1837. *Hortus Mauritianus ou Enumération des plantes exotiques et indigènes qui croissent à l'Île Maurice.*
- (2) BAKER, J. G. 1877. *Flora of Mauritius and the Seychelles.*
- (3) JOHNSTON, H. H. 1895. Additions to the Flora of Mauritius as recorded in Baker's *Flora of Mauritius and the Seychelles.* *Trans. Bot. Soc. Edinb.* xx, pp. 391-407.

South African species of *Riella*, including an account of the developmental stages of three of the species. By GRACE WIGGLESWORTH, M.Sc. (Communicated by Prof. F. E. WEISS, F.R.S., F.L.S.)

(With 58 figures in the text)

[Read 7 May 1936]

THE members of the genus *Riella* are conspicuous amongst the Hepaticae on account of their peculiar form and manner of growth. They are aquatic plants, growing in brackish or fresh water.

Allorge (1932) has worked out the distribution of the known species of *Riella*. He dealt with thirteen species, some of which had only been collected a few times. North Africa, with seven species in its flora, had proved to be the richest collecting-ground, and our knowledge of these forms is largely due to Trabut. He not only revised the known species of *Riella* and added descriptions of new forms, but supplied Goebel with material for morphological investigations of the genus.

The seven species, native of N. Africa, are *R. helicophylla* Mont., *R. Parisii* Gott., *R. Cossioniana* Trab., *R. bialata* Trab., *R. Reuteri* Mont. f. *Battandieri* Trab., *R. numidica* Trab., and *R. sersuensis* Trab. *R. Reuteri* Mont. occurs in Southern Europe as two local forms—*R. Reuteri* forma *lemanica* Trab. and *R. Reuteri* forma *gallica* Trab. Trabut (1911) considered that the other European species—*R. Notarisii* Mont.—may also be a form of the same species, but the meagreness of Montagne's description and lack of more material prevented the proof of this suspicion.

Apart from N. Africa, one species, *R. affinis* Howe & Underw. from Grand Canary has been described, and another, *R. americana* Howe & Underw. from N. America. *R. Paulsenii* Porsild, is only known from a culture made from dried mud collected at Bokhara in Turkestan and sent to Copenhagen for the investigation of crustacea. The discovery of another species at Lahore—*R. indica* Steph.*—suggests that more may be forthcoming from other parts of the world where suitable conditions exist. According to Sims (1926, 1927) only one species of *Riella*, *R. capensis* Cavers, has been distinguished in S. Africa, and this, like the Bokhara material, was first found accidentally. Spores happened to be included in some dried mud sent from its native locality to England for the investigation of crustacea; the mud produced, in addition to small crustacea, a good crop of *Riella* plants which were investigated by

* *R. indica* Steph., cited by Allorge, appears to be the species described as “*R. indicast.*, n. sp.”, by Kashyap (1917).

Cavers (1903). He described it in 1903, giving it the name *R. capensis*, because the mud which contained the spores was taken from a pool at Port Elizabeth in Cape Colony. The plants thus obtained grew vigorously in small dishes in the Department of Botany in the University of Manchester. They were propagated by means of spores, and after flourishing for about eight years dwindled out. In 1926 a number of plants of *Riella*, together with *Hydrodictyon africanum* and other algae, were reared in the Cryptogamic Laboratory at the Manchester University from other samples of mud from S. Africa, sent by Miss Stephens. It was noticed that these plants differed in several respects from those described by Cavers, of which some preserved material remains in Manchester. The purple colour of the spores and the nature of their spiny covering suggested that this might be a new species. Since then the plants have been grown successfully for ten years, fruiting freely and maintaining their distinguishing characters. In 1932 more dried mud and preserved material from several sources was received from Miss Stephens. Most of the plants were collected near Cape Town, and are probably representatives of different species of *Riella* recorded as *R. capensis* by Sims (1926). The material sent by Miss Stephens included three species of *Riella* from the Cape : (1) the form with purple spores mentioned above ; (2) a form with brown, winged spores ; and (3) a peculiar shrubby form. The plants included in (3) had no ripe spores, but one bore immature capsules. Spines were present, but not fully formed, on the spores which were still in tetrads.

Preserved and dry material of another species obtained from mud collected from a large salt-pan near Brandfort in Orange Free State was also sent by Miss Stephens. The spores of this species approach in size those of the other S. African species, but the spines are more numerous and finer, and they arise from less well-defined reticulate thickenings on the outer spore-coat.

It is proposed in the following account to call the two distinct species from the Cape, of which there was both material sent from S. Africa and plants obtained by culture of the spores, *Riella purpureospora* and *R. alatospora*. The other form, represented by a few individuals collected by Miss Stephens in Valkenberg vlei, possesses distinctive characters in its vegetative form. It may prove to be a distinct species, and in this account of the S. African species of *Riella* will be called the ' *Riella* from Valkenberg vlei'. It was growing in deeper water than the other species collected by Miss Stephens, and it is possible that it is a monstrous form. The species from Brandfort, which has finer spines, will be described under the name of *R. echinospora*. Miss Stephens (1929) describes the conditions under which the species of *Riella* occurring near Cape Town grow. She says they occur in temporary pools (vleis) on the Cape Flats, where they appear sporadically. This stretch of land appears to be an isthmus most of which was submerged in the sea until comparatively recent geological times. It is now covered by a surface layer of blown sand, mostly fixed by the vegetation, over clay-slate in the northern half and granite in the southern. It is dry in the summer, but with the coming of the rains in April and May

depressions in this substratum become filled with water, and before long *Riella* and *Hydrodictyon* may be seen growing intermingled with Charophyta and submerged *Crassula* and *Salicornia*. During September the rainfall begins to get less, and by the end of the year the water is dried up and the surface remains dry for some months.

In order to obtain early stages for morphological investigation and to ascertain whether the new forms retained their diagnostic characters portions of dried mud, detached spores, and portions of dried plants bearing sporogonia have been cultivated in water from time to time. Glass vessels of various sizes were used. The largest was 18×11 in. with about 6 in. depth of water, but smaller ones, about 3 in. in diameter with 1½–3 in. of water were quite as successful. Tap-water, on loam which had been washed with boiling water, together with a little washed sea-sand, proved a suitable medium. The vessels were put in a north or a west window.

Having taken advantage of the facilities offered for examining material of *R. capensis* Cavers, which has been preserved in Manchester, an emended diagnosis of this species has been added to those of the new species, type-specimens of which have been deposited in the Herbarium of the University of Manchester. Also, it has been thought worth while to add the tentative key to all the known species of *Riella* which now follows.

TENTATIVE KEY TO THE SPECIES OF *RIELLA*.

- Two-winged axis (Trabut, 1909) *bialata*.
- One-winged axis.
 - Large spores (100 μ or over, including spines).
 - Spores purple or crimson *purpureospora*.
 - Spores brown.
 - Spores winged *alatospora*.
 - Spores without wing.
 - Involucre winged (Howe & Underwood, 1903) *affinis*.
 - Involucra without wings.
 - Spines arising from reticulate thickening on spore (Howe & Underwood, 1903).
 - Spines 10–24 μ sometimes curved, enlarged at ends *americana*.
 - Spines shorter, straight, sometimes acute *capensis*.
 - Reticulations on spore absent or slight.
 - Spines distant, enlarged at ends *helicophylla*.
 - Spines more numerous, acute or truncate *echinospora*.
 - Small spores (usually less than 100 μ).
 - Spines arising from reticulate thickening on the spore.
 - Comparatively large plants (up to 20 cm.) with large leaf-scales *Parisii (Clauzonis)*.
 - Smaller plants (less than 10 cm.).
 - Leaf-scales lanceolate, involucra papillate.
 - Involucra cylindrical, plants 10 mm. or less (Kashyap, 1917) *indica*.
 - Involucres ovoid or subcylindrical, larger plants (Trabut, 1935) *sersuensis*.

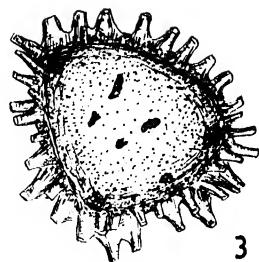
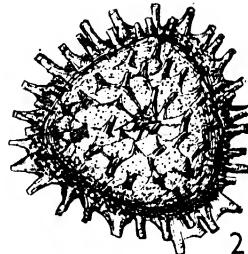
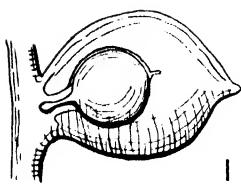
Leaf-scales short and wide (except in emerged forms).	
Involucrum smooth or only papillate at orifice	<i>Reuteri.</i>
Spores without reticulate thickening.	
Involucrum winged.	
Spores with conical tubercles, short and subobtuse (Porsild, 1903)	<i>Paulsenii.</i>
Spores with truncate spines, sometimes dilated at the apex (Trabut, 1887)	<i>Cossoniana.</i>
Involucrum without wings.	
Minute plants (5–15 mm.) with conspicuous lanceolate leaf-scales (Müller, 1908)	<i>Notariisii.</i>
Larger plants (10–40 mm.) frequently with 2–3 spiral turns in the thallus, leaf-scales small.	
Involucrum beaked, spines of spores long and enlarged at the ends	<i>helicophylla.</i>
Involucrum not beaked, spores smaller (60–80 μ), spines acute or obtuse (Trabut, 1935)	<i>numidica.</i>

RIELLA PURPUREOSPORA, sp. n.

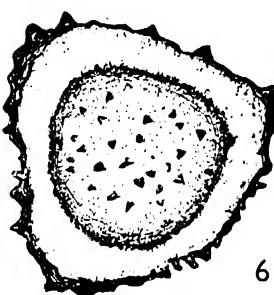
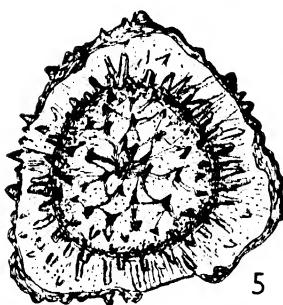
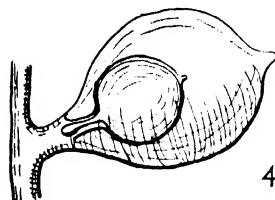
Dioica. *Frons* erecta, circa 3·5–6 cm. longa, plerumque parum ramosa. *Costa* circa 0·4 mm. lata; ala ad 1·6 mm. lata, undulata, basin versus sensim angustata, basi nuda. *Squamae costales* variiformes, circa 0·4–0·9 mm. longa, 0·3–0·6 mm. lata. *Antheridia* in margine alae seriata. *Involucra* ad 2 mm. longa, piriformia vel subglobosa, haud raro cellulis prominentibus; apex ad culmen parvus. *Sporae* circa 112 μ (spinis inclusis) reticulatae, purpureae, tetraedrae, spinis circa 12 μ longis crassis truncatis.

Hab. AFRICA AUSTRALIS; prope Cape Town *E. L. Stephens* legit; atque usu sporarum illae originis coluit *G. Wigglesworth*.

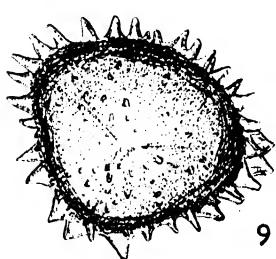
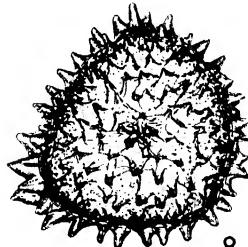
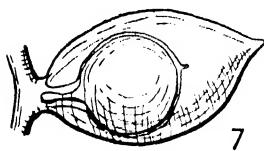
In favourable cases some of the spores began to germinate in three days after submergence in water. Fig. 13 shows a young stage where the spore-coat is still attached to the germ-tube. Here the upper cells of the single row which was first formed, have divided by vertical and horizontal divisions. A spathulate thallus, one layer of cells in thickness, has been produced which tapers down to the single row of cells at the base. From this region two rhizoids have grown down into the substratum. The division walls in the upper region are usually laid down regularly; they form two inner rows and a marginal series. In the latter oblique walls are formed occasionally and sometimes a few divisions can be seen in the inner cells as shown in the plant figured. The marginal cells about half-way down on the left-hand side, have begun to divide further in this plant. The inner two rows of cells often undergo no further division, and the activity of the marginal cells usually ceases about this stage in the upper nine or ten tiers. The cells near the base of the blade-like portion divide more frequently, with the result that the thallus becomes wider in this region. The cells of the basal filament remain as a single row except where they approach the rapidly broadening portion. Here a few divisions take place, and above this a longer or shorter stalk is formed below the blade-like upper part. The stalk itself undergoes further growth and division, but to



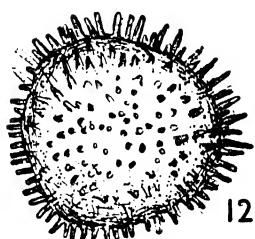
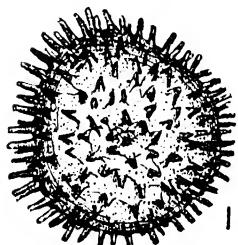
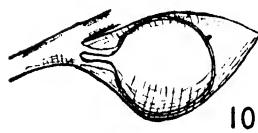
R. PURPUREOSPORA



R. ALATOSPORA



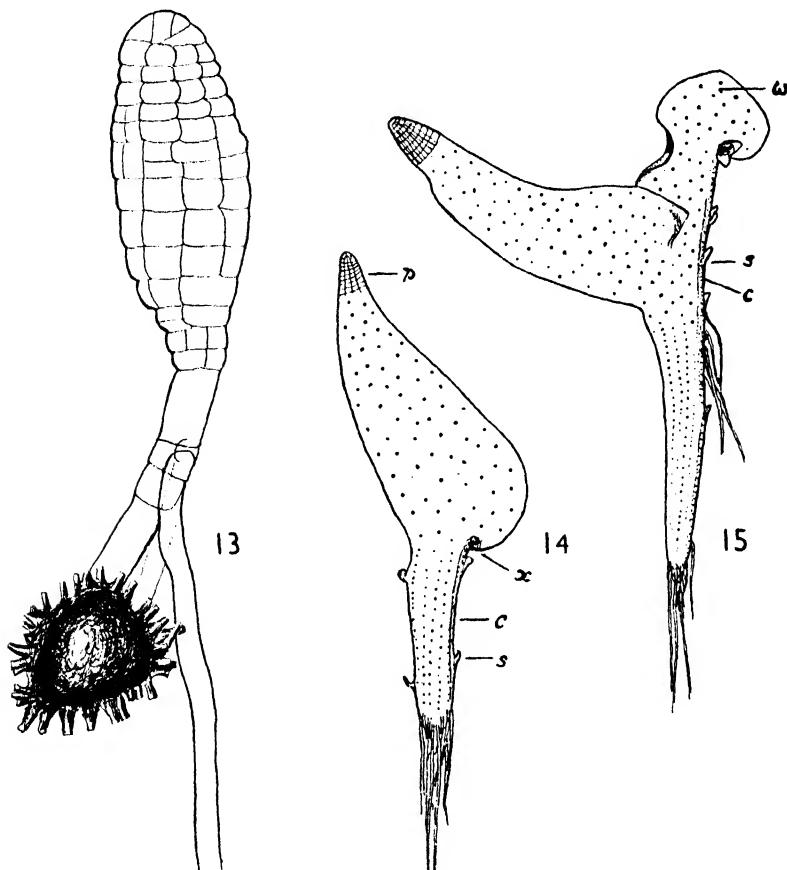
R. CAPENSIS



R. ECHINOSPORA.

Figs. 1-12 showing chief diagnostic characters of the South African species of *Riella*.
1, 4, 7, 10 show involucel attached to a portion of the axis, $\times 13\frac{1}{2}$; 2, 5, 8, 11,
outer face of spore, $\times 300$; 3, 6, 9, 12, inner face of spore, $\times 300$.

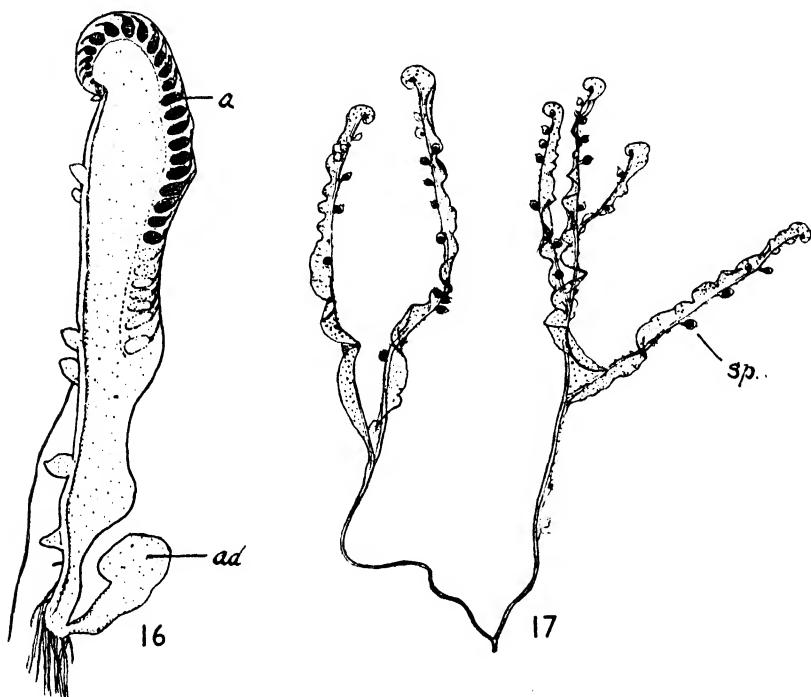
a less degree than in the blade-like upper portion. In this species the cells on one side of the primary thallus are usually more active than those on the other and a unilateral structure such as that shown in fig. 14 is produced. Here cell-division, proceeding in a third dimension at x in fig. 14, will continue a rib already formed on the same side, along the margin of the stalk (c),



Figs. 13-15.—*Riella purpureospora*. 13. A germ-plant with spore still attached to germinating tube, $\times 180$. 14. An older stage of the primary thallus, $\times 13\frac{1}{2}$. 15. The first appearance of a winged shoot on the primary thallus, $\times 13\frac{1}{2}$. c , rib; p , primary thallus; s , leaf-scale; w , winged shoot; x , intercalary growing point.

where lengthening cells form conducting tissue. Occasionally a similar development takes place on the opposite side, and in this case the bilateral symmetry of the plant is maintained for a longer period than usual. At x in fig. 14 an intercalary growing point has now been established, and definite appendicular organs have begun to appear. In the plant figured, single rudi-

mentary scale-leaves are present on the stalk of the primary thallus and pairs of scale-leaves protect the intercalary growing point. Usually at this stage a single apical cell could not be distinguished. Immediately above the growing point in fig. 14 a protuberance indicates the beginning of the wing, which is characteristic of the adult shoot. Wing-tissue and axis-tissue arise almost simultaneously. More frequent division occurs in the wing, especially at the margin, with the result that an undulate membrane is formed. The wing is one cell thick, except where it approaches the rib (or axis) : in the latter, division occurs in three dimensions. In fig. 15 the adult form of shoot initiated

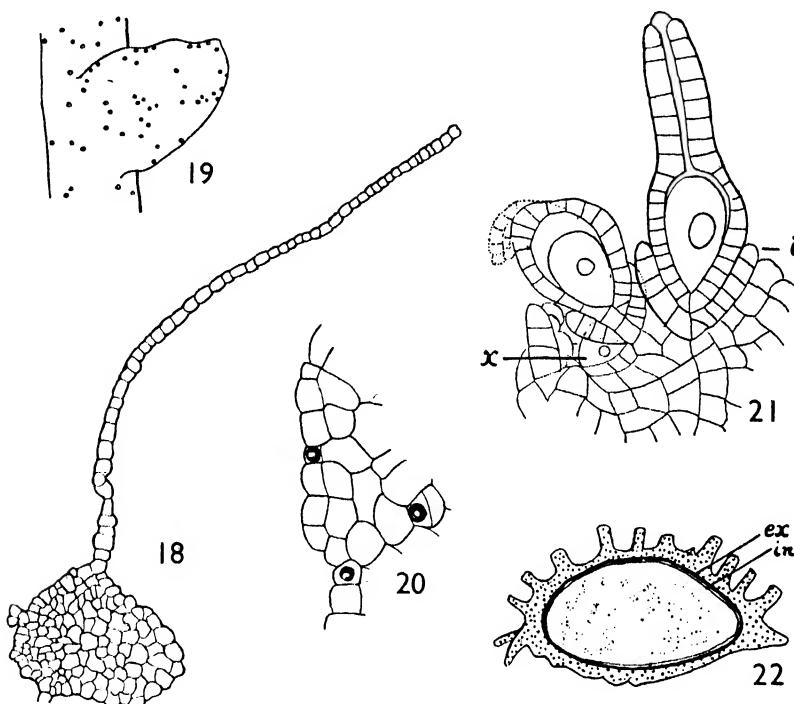


Figs. 16, 17.—*Riella purpureospora*. 16. A male plant, $\times 13\frac{1}{2}$. 17. A female plant, nat. size. a, antheridium; ad, adventitious shoot; sp., sporogonium, enclosed in involucrum.

by the intercalary growing point is shown. It has pushed aside the upper part of the primary thallus, which has increased considerably in size, except at the tip. The bilateral symmetry of the plant has now been destroyed. The growing point of the secondary shoot is overtopped by the rapidly growing wing, which is continuous with the membranous tissue below.

Figs. 16-17 show mature plants. The male plant (fig. 16) has a small adventitious shoot (ad) at the base. Adventitious shoots were formed to a limited extent on plants of either sex, at no definite position on the axis.

The female plants were usually larger than the male plants ; the one shown in fig. 17 had reached a length of 9 cm., but most of the plants were shorter than this. In fig. 17 the rooting base has become detached. The thallus grows vertically upwards in the water and is usually simple or sparingly branched. The axis or rib is about 0·4 mm. in breadth. It is slightly flattened on the ventral side and drawn out into a wing on the dorsal side as shown in fig. 18. The wing is undulate. It is broadest in the falcate portion above the growing point,



Figs. 18-22.—*Riella purpureospora*. 18. Transverse section of winged axis, $\times 43\frac{1}{2}$. 19. Portion of axis bearing a leaf-scale; distribution of oil-cells shown, $\times 43\frac{1}{2}$. 20. Oil-cells on a portion of a leaf-scale, $\times 180$. 21. Growing point of an adventitious shoot, showing archegonia and beginning of the involucrum (*i*), $\times 300$. 22. Transverse section of a spore, $\times 300$. The outer face of the spore is above. *ex*, extine; *in*, intine.

where it may reach as much as 1·6 mm., and narrows down towards the base, leaving the lowest portion of the axis wingless. The cells vary in size and shape, but are more elongate near the rib, and are smaller and more regular near the margin. The rhizoids grow chiefly from cells at the base of the axis, but occur sparingly higher up the plant. The scales on the axis are small, tongue-shaped or triangular appendages containing chlorophyll, about 0·5-0·9 mm. in length, and usually a little less in breadth. They are attached obliquely or vertically

to the sides of the axis and become situated singly or in pairs at irregular intervals. Scales, axis, and wing are provided with oil-containing cells (see figs. 19 & 20), which are scattered irregularly over the surface. The single oil-body which each of these cells produces is only seen in fresh healthy specimens.

The female plants give rise to a large number of sporogonia (*sp* in fig. 17). Archegonia are produced in acropetal succession and an involucro (*i*) grows from the axis round each as shown in fig. 21. At the growing point which is here represented, there appears to be a definite apical cell (*x*). The involucro (*i*) is beginning to envelop a young archegonium on the right. A younger archegonium lies nearer the apical cell. In this figure, which represents an optical section, the cells in the plane below the apical cell are not shown. If fertilization fails the involucro is arrested in growth and it may form a small sac ; otherwise it enlarges and completely encloses the developing sporogonium, leaving a large space in between. It becomes subglobose in shape (see fig. 1), and at the distal end it narrows rather suddenly into a little beak, the open termination of which is surrounded by an irregularly protruding row of cells. The involucro may reach as much as 2·5 mm. in length, but is often less. The venter of the archegonium keeps pace in growth with the developing sporogonium investing the foot and shortly stalked capsule ; the neck is pushed to one side or remains at the top as a small brown projection.

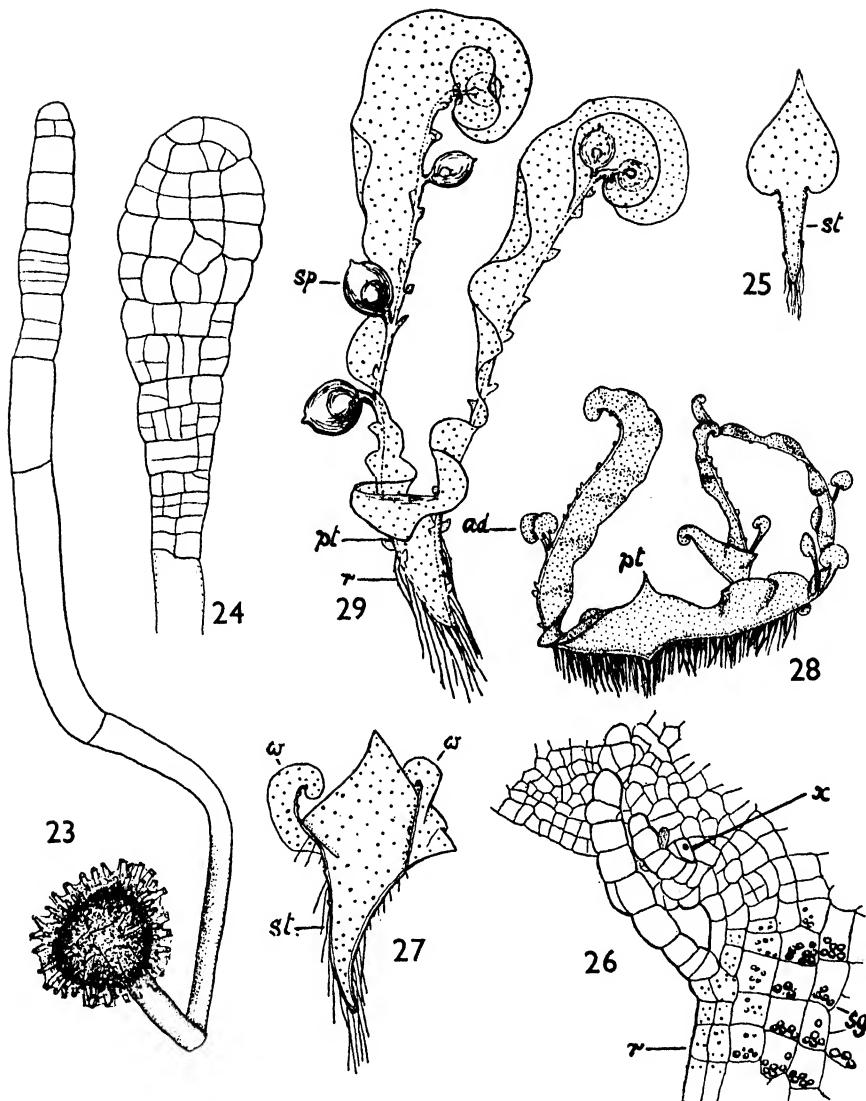
The capsule is spherical, about 0·8 mm. in diameter. It is connected with a well-developed foot by a short row of cells, seta and foot together measuring about 0·3 mm. in length. When mature the capsule contains spores mixed with sterile cells, many of which contain starch-grains. The spores are purple, sometimes crimson in colour, about 112μ in greatest width. They are approximately triangular when viewed from the outer side, as shown in figs. 2 and 3, and elliptical in section, as shown in fig. 22. On the outer side they are covered with stout truncate spines about 12μ in length, connected by basal membranes. The inner face, shown in fig. 3, bears a few isolated short spines and irregular protuberances.

RIELLA ALATOSPORA, sp. n.

Dioica. Frons erecta, circa 3·5 mm. longa, multo ramosa, saepe arbustuliformis. Costa circa 0·25 mm. lata ; ala ad 3·5 mm. lata, undulata, saepe basi porrecta. Squamae costales variiformes, circa 0·5×0·4 mm. Antheridia in margine alae seriata. Involucra ad 2 mm. subspherica vel oblongo-oviformia, cellulis non multum prominentibus ; apex ad culmen parvus, brevissime pedicellatus. Sporae alatae, brunneae, circa 120 μ (ala inclusa), reticulatae, tetraedrae vel rotundae, spinis circa 8 μ longis obtusis vel acutis ; ala aliquantum spinosa.

Hab. AFRICA AUSTRALIS ; prope Cape Town E. L. Stephens legit, atque usu sporarum illae originis coluit G. Wigglesworth.

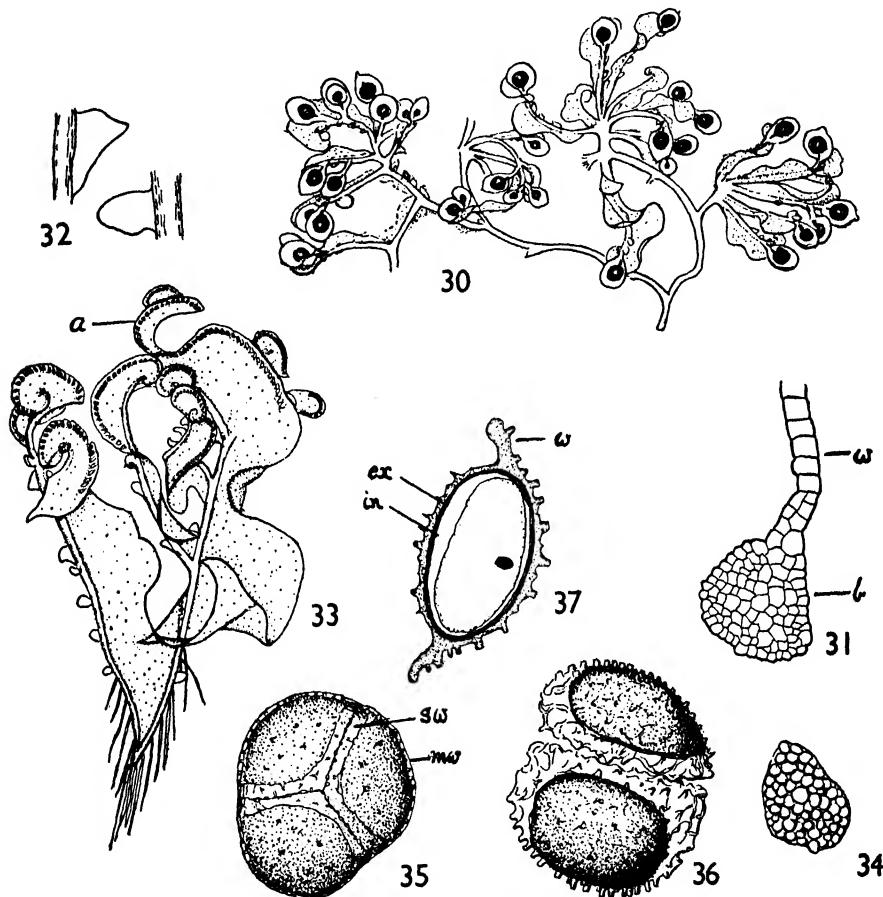
The original locality was a vlei at Salt River between the main road and a railway line.



Figs. 23-29.—*Riella alatospora*. 23. Germ-plant with spore attached, $\times 180$. The membranous part of the wing of the spore has decayed, leaving the main thickenings. 24. Upper region of a primary thallus at a later stage, $\times 180$. 25. A bilateral young plant with two intercalary growing points, $\times 4$ approx. 26. Intercalary growing point (x) in optical section, $\times 300$. 27. Young plant with two lateral winged shoots (w) arising from the primary thallus, $\times 4$ approx. 28. Older plant with many adventitious shoots, $\times 4$ approx. 29. Female plant with two almost equal lateral shoots, one bearing ripening sporogonia, $\times 4$ approx. ad , adventitious shoot; pt , primary thallus; st , stalk of primary thallus; sg , starch-grains; sp , sporogonium; r , rib-cells; w , winged shoot; x , apical cell.

The earliest stages of growth in this species resemble those of *R. purpureospora*. The germ-tube breaks through the outer face of the spore, which has lost by this time the membranous part of its wing by decay. A filamentous stage (fig. 23) is followed by a spathulate stage. Fig. 24 shows the upper portion of this, slightly more advanced than the corresponding part in the young plant of *R. purpureospora* shown in fig. 13. After this stage there was a striking difference in the appearance of the whole culture compared with that of *R. purpureospora*. The majority of the plants of *R. alatospora* became heart-shaped at the top instead of protruding at only one side as was usual in *R. purpureospora*. One of these is shown in fig. 25. Here there is a fairly long stalk (*st*) with rudimentary leaf-scales and rib-tissue on each side extending to the intercalary growing points which lie at the junction of the stalk and the broadening part of the thallus. Fig. 26 shows the growing region in another plant where there is the appearance of an apical cell (*x*). Usually no definite apical cell could be distinguished until the adult form of shoot had been established for some time. Large starch-grains (*sg*) were present in the basal regions of the central cells of the stalk in this plant, while the rib-tissue (*r*) contained very small scattered grains. The establishment of two intercalary growing points is followed by the upward growth of two similar shoots (*w*) as shown in fig. 27. The wings of these shoots are continuous with the median membranous tissue which connects the tip of the primary thallus (*pt*) with the base of the plant. The part which was stalk in the primary thallus widens into a V-shape, the two side ribs of which are continuous with those of the secondary shoots (*w*). The latter may ascend at once or may diverge for a time on account of the extension of the intermediate tissue as shown in fig. 28. The original tip of the primary thallus usually becomes displaced, and together with a portion of the intermediate tissue lies more or less at right angles to the main part of the plant and not in the same plane as shown in fig. 28. In this plant a forking of the right-hand shoot has occurred, and both right and left main shoots have produced adventitious shoots (*ad*) singly or in pairs. Each of these consists of a stalk terminated by a plate-like membranous structure. At the junction of the stalk and plate two growing points are usually formed. Where there is only one the plate is asymmetrical in form. This kind of shoot to some extent recapitulates the early developmental story, the intercalary growing points giving rise to the adult form of shoot with a wingless portion at the base. The amount of adventitious branching and apical branching varies with the individual. Fig. 29 shows a plant which is still bilateral, with two approximately equal shoots connected by an intermediate membranous portion, the free distal end (*pt*) of which is bent back. This plant has produced sporogonia (*sp*) and is about 2 cm. in length. Older plants, sent dry from S. Africa, reached 3·5 cm. in length. One of these, soaked out, is shown in fig. 30. This plant bore clusters of branches and had a shrub-like form. The basal part of the axis is naked, but this, to some measure, is due to decay of the more delicate membranous tissue. The axis, of which a transverse section is shown in fig. 31,

is about 0.35 mm. in breadth. It merges gradually into the wing, which is composed of two layers of cells where it meets the axis. The peripheral cells of the axis, as in *R. purpureospora*, are shorter than the central cells, and some



Figs. 30-37.—*Riella alatospora*. 30. Old female plant showing a shrubby growth, $\times 4$ approx. 31. Transverse section of the winged axis, $\times 43\frac{1}{2}$. 32. Leaf-scales, $\times 13$. 33. Male plant repeatedly branched, $\times 4$ approx. 34. Sterile cell from an immature capsule, $\times 225$. 35, 36. Parts of spore-tetrads before complete separation (two stages), $\times 225$. 37. Transverse section of a spore, with the external face to the right, $\times 300$. *a*, antheridia; *b*, axis; *w*, wing; *ex*, extine; *in*, intine; *mw*, mother-cell wall of the tetrad; *sw*, 'special wall'.

of them give rise to oil-cells. The wing reaches about 3.4 mm. in greatest width and is more or less undulate. The leaf-scales, fig. 32, like those of *R. purpureospora*, are small; they are about 0.5 mm. long and 0.4 mm. broad. They are

attached vertically or obliquely to the axis, and are sometimes decurrent. They vary in shape.

The plants are dioecious. The male plants are often smaller than the female plants, although the one shown in the fig. 33 is quite as large. Antheridia are borne in series and become embedded in pockets in the hem of the wing. The female plants, of which two are shown in figs. 29 and 30, produce one or more sporogonia on each branch. The subspherical involucre which surrounds each sporogonium (see fig. 4) is 2 mm. or less in length. It is contracted where it meets the short stalk attaching it to the axis. Many of the cells project slightly outwards, especially round the orifice, which terminates a short beak at the distal end. The capsule may reach as much as 0·9 mm. in diameter; the foot and seta together measure about 0·4 mm. in length. The spores, two of which are shown in figs. 5 and 6, are about 120μ in greatest width, including the wing with which they are provided. They are brown in colour and bear numerous spines, about 8μ long, with well-marked basal connecting membranes forming reticulations on the outer face. Spines are also present on the wing, as shown in fig. 5, but they are shorter than those on the body of the spore. Striations are also present in the wing; they tend to radiate outwards from the body of the spore, except at the edge, where they help to form the thickened spiny border (see fig. 5). The inner face of the spore, shown in fig. 6, bears a few isolated short spines which are confined to the body of the spore.

The wing of the spore, which is about 24μ in greatest width in the mature spore, is slightly concave, as shown in transverse section illustrated in fig. 37. It is a portion of the 'special wall' of the tetrad, figures of which are shown (figs. 35 & 36). Its origin is discussed later (pp. 328-9).

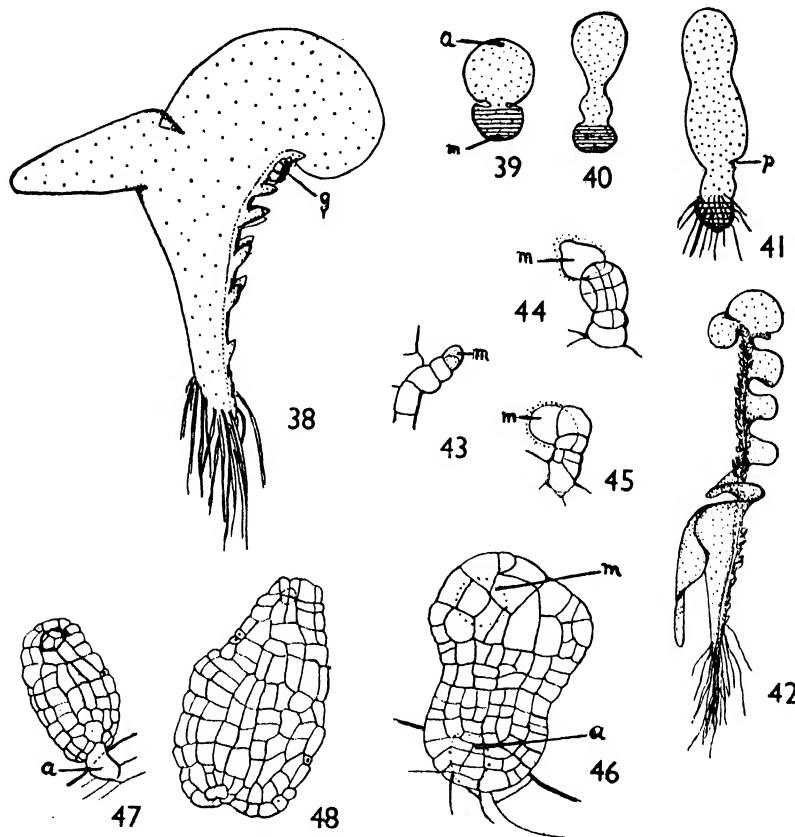
RIELLA ECHINOSPORA, sp. n.

Dioica. Frons 1-3·5 cm. longa, 0·5-3 mm. lata, plerumque simplex. *Costa* circa sexta pars frondis latitudine; ala multum undulata, ad basin subnulla. *Squamae costales* variiformes, ad 0·48 mm. longa, 0·31 mm. lata, basales multo minores, aggregatae vel distantes, aliquando cum gemmis et squamis ventralibus intermixtae. *Antheridia* in margine alae seriata. *Planta feminea* 1-5 sporogonia pariens. *Involucra* ovoidea acuminata, superficie levia. *Sporae* brunneae, subrotundae, spinosae, circa 100μ (spinis inclusis) debiliter reticulatae, spinis exterioris faciei circa $13\cdot2\mu$, interioris faciei circa $6\cdot6\mu$.

Hab. AFRICA AUSTRALIS; Orange Free State, Schonken's Salt Pan, prope Brandfort, Stephens et Wigglesworth coluerunt.

This species proved interesting as it differed from the other species from S. Africa in its method of vegetative reproduction. The first successful plant, obtained from cultivation of the dry material sent by Miss Stephens, began to produce gemmae at a very early stage in the growth of the secondary thallus (see fig. 38). The gemmae became detached; some of these fell to the bottom of the jar in which they were growing and ultimately formed new plants. Some were removed to other jars to form new cultures. They were laid on damp mud,

and water gradually added. At first only gemmiferous plants were produced, but later new plants producing ripe sporogonia were obtained both from fresh sowings of dried material and from gemmae produced in earlier cultures. Some of the gemmiferous plants failed to produce sporogonia and grew very luxuriantly,



Figs. 38-48.—*Riella echinospora*. 38. Young plant beginning to produce gemmae (*g*), $\times 7$. 39-41. Gemmae at different stages of growth; the shaded basal part corresponds to the distal end on the gemma in the previous figure; *p* is the growing point of the secondary thallus; $\times 13$. 42. Older gemmiferous plant, $\times 4\frac{1}{2}$. 43-46. Trichome and other ventral appendages representing stages in the development of a gemma, $\times 225$. 47. A ventral scale, $\times 70$. 48. A lateral leaf-scale, $\times 70$.

producing plants more than twice the size of the fertile plants. Such plants sometimes branched freely, a feature which was unusual in fertile plants of this species.

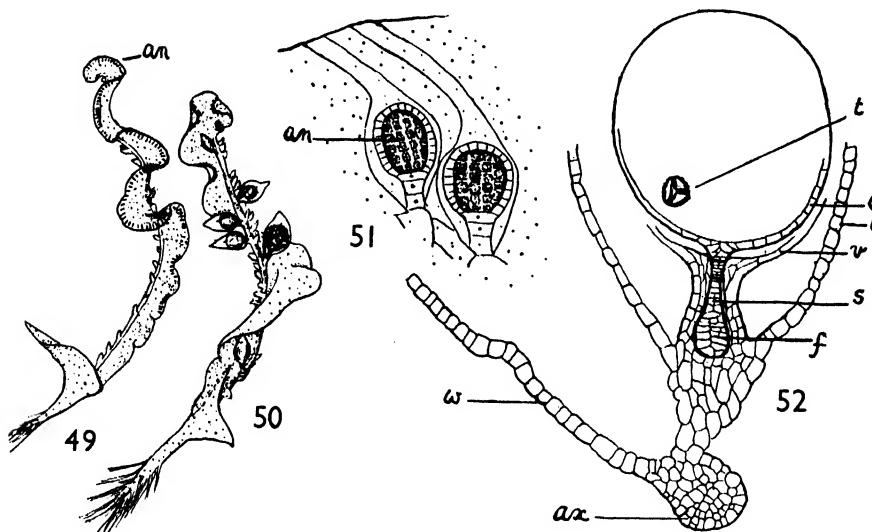
Gemmae were formed on the axis ventrally to the leaves. They showed the form of a constricted plate before they became detached. The proximal part was attached by a single cell, above the base, on the ventral side,

the distal part (shaded in the figures) bore a spherical mucilage cell below the apex on the same side. Most of the cells in both upper and lower parts were crowded with starch. The development of the gemma can be gauged by examining various ventral appendages such as those shown in figs. 43–46. These were obtained from various parts of the axis. The trichome (fig. 43), showing the earliest stage, bears the mucilage cell at one end and the attachment cell at the other. In fig. 46 the mucilage and attachment cells have become overgrown by neighbouring cells and are represented by dotted boundaries (*m*). A lateral leaf-scale (see fig. 48) did not differ much from a ventral scale, such as that shown in fig. 47, except that it was generally attached by several cells to the axis. Mucilage cells were not often obvious at the tip of the leaves when mature. Both leaf-scales and ventral scales were concave and bore oil-cells at frequent intervals at the margin.

The further development of the gemma when detached is illustrated in figs. 39–41. The part that was the distal end when the gemma was attached (fig. 38) became the lower part of the rooted base of the new plant. The part that was attached became the assimilating portion of the primary thallus. Important changes took place in the constricted area between the two regions, which resulted in its elongation and sooner or later in the establishment of a definite growing-point at its upper end (*p* in fig. 41). The development of the secondary axis from this point followed much the same course as that occurring in plants of *R. purpureospora* when it had reached the corresponding stage in its development from the spore, except that there was a remarkable difference in the plants, which were gemmiferous, as regards their leafy appendages. In addition to definite gemmae *R. echinospora* bore numerous ventral leaf-scales as well as to the ordinary lateral leaves. Sexual reproductive organs were produced on some of the gemmiferous plants, but were usually abortive when gemmae were numerous. The involucre surrounding the aborted archegonium often reached the length and breadth of a leaf-scale, and with its chlorophyllose cells added to the assimilating tissue of the plant.

In the fertile plants reproductive organs were borne, as shown in figs. 49–52. The leafy appendages were in many cases augmented by ventral leaf-scales. Three rows of leaves were not uncommon, and additional ones at the base were frequent. The male plants were often smaller than the female plants. The series of antheridia borne in pockets (see figs. 49 & 51) near the margin of the wing was continuous, or interrupted, as shown in the plant represented in fig. 49. Both this and the female plant shown in fig. 50 were grown in S. Africa. The plants cultivated in Manchester were often larger. It appears that reduction in intensity of light favours more luxuriant vegetative growth. The relation of the sporogonium to the axis and wing is shown in figs. 50 and 52. The whole of the section of the wing, which is about five times the breadth of the axis, is not shown in fig. 52, and only the lower portions of the venter of the archegonium and the involucre are shown. The involucre was ovoid, tapering at both ends as shown in figs. 10 and 50. The seta and foot (*s* and *f* in fig. 52)

together measured about 0.35 mm. in length. The spores sometimes varied in size in a single capsule in this species. The spines on the spores; examples of which are shown in fig. 11, were more numerous both on the outer and the inner side of the spore than was the case in the other S. African species; also the kind of spine on the two faces showed a great resemblance in this species, although they were distinctly shorter on the inner face. The ridges forming reticulations on the outer side of the spore were only slightly developed in this species. As in the other species, there were no reticulations on the inner face of the spore.



FIGS. 49-52.—*Riella echinospora*. 49. Male plant, $\times 4\frac{1}{2}$. 50. Female plant with ripe sporogonia, $\times 4\frac{1}{2}$. 51. Portion of wing bearing two pockets containing young antheridia, $\times 180$. 52. Transverse section of axis bearing a ripe sporogonium, $\times 44$. *an*, antheridium; *ax*, axis; *c*, wall of capsule; *i*, involucr; *f*, foot; *s*, seta; *v*, venter of archegonium; *t*, spore tetrad; *w*, wing.

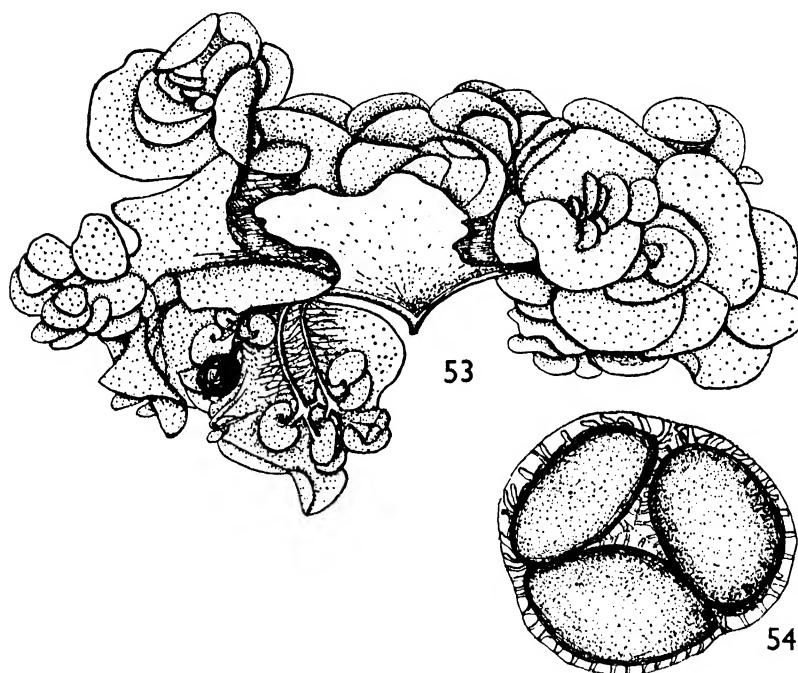
RIELLA sp. from Valkenberg vlei.

The germination of this species has not been observed. The description of the mature plant is made from a few specimens which were preserved in formalin. One of these plants is represented in fig. 53. The thallus is about 1 cm. high and greater in width. It appears to have had two intercalary growing points on the primary thallus, for a broad median membrane separates two ribs which diverge from the base (cf. the development of *R. alatospora*).

The halves of the plant have branched several times and each has produced a large number of adventitious branches. These are at various stages of development and are so crowded that they have produced a cauliflower-like

form of plant. In this plant there is proliferation at the apex of some of the shoots, as shown at (p) in fig. 55. Several of the older adventitious branches have been removed so as to expose the wing and axis, and in order to show the sporogonia (*sp*) and sterile involucres which it has produced.

The axis in this species is about 0.5 mm. in width and the wing reaches 4 mm. in breadth. The cells are considerably larger than those in *R. purpureospora* and *R. alatospora*, making the texture of the wing stouter. The margin of the wing is irregular and has an eroded appearance. The leaf-scales are



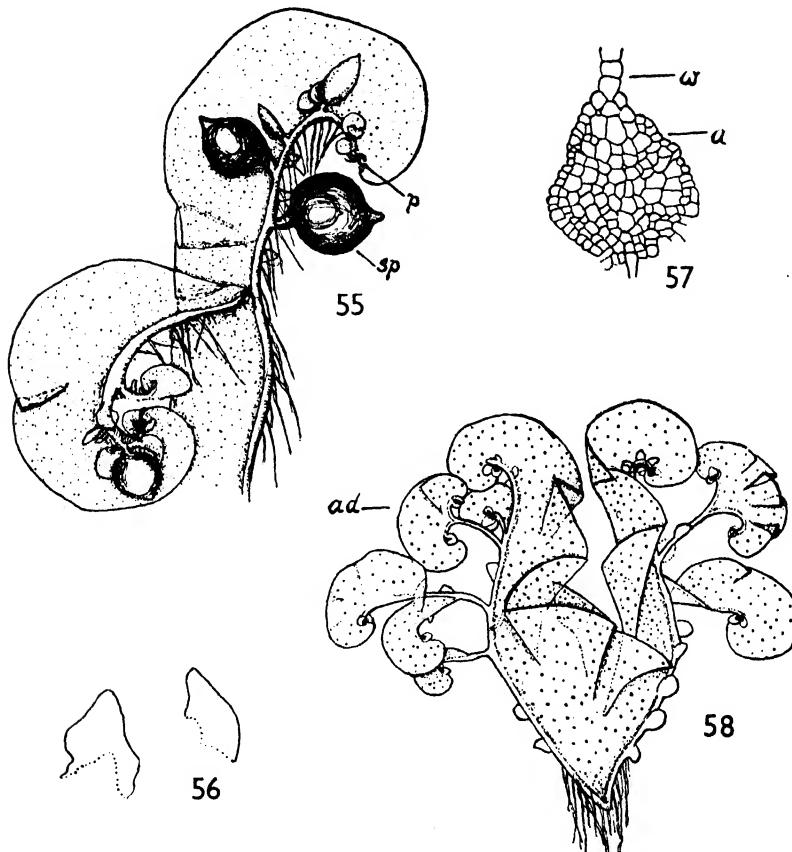
Figs. 53, 54.—*Riella* from Valkenberg vlei. 53. A plant with the left side arranged to show adventitious shoots and a sporogonium surrounded by its involucres, $\times 4$ approx. 54. Spore tetrad, $\times 300$.

very variable, as shown in fig. 56. Some are much elongated, reaching 1 mm. in length, others are much shorter and may be almost as wide as long. Like those of the other species they are attached by a broad base either vertically or obliquely to the axis, and some are decurrent.

Antheridia have not been seen in this species.

The sporogonia are all immature, but one or two showed the tetrad stage (see fig. 54). The involucres surrounding the sporogonia are subspherical and seated on short stout pedicels, as shown in fig. 55. The largest measured 3 mm. in diameter. No capsules which had reached more than 1.4 mm. in

diameter were seen. The oldest spore examined measured 78μ in greatest width. This measurement included the spines, which were unthickened and slightly bent inside the cell-wall of the tetrad. Without the spines the spore measured 72μ .



Figs. 55-58.—*Riella* from Valkenberg vlei and *R. capense*. 55. A portion of the thallus of the *Riella* from Valkenberg vlei with some of the adventitious branches removed. Proliferation (*p*) at the apex is indicated. Also two involucres containing sporogonia (*sp*) and an empty involucre are shown, $\times 4$ approx. 56. Leaf-scales of the *Riella* from Valkenberg vlei, $\times 13$ approx. 57. Transverse section of winged axis of the *Riella* from Valkenberg vlei. An adventitious branch has been detached from the ventral side, $\times 43\frac{1}{2}$: *a*, axis; *w*, wing. 58. A plant of *R. capense* showing adventitious shoots (*ad*) on a bilateral thallus, $\times 7\frac{1}{2}$.

RIELLA CAPENSIS Cavers, emend.

Dioica. Frons erecta, 1-3 cm. longa, multum ramosa, saepe arbusculiformis. Costa 0.2-0.4 mm. lata; ala 3-4 mm. lata, saepe basi porrecta, valde undulata,

Squamae costales variiformes. *Antheridia* in margine alae seriata. *Involucra* circa 2.5×1.2 mm., ovoideo-acuminata, superficie levia. *Capsula* globosa, circa 0.8 mm. *Sporae* brunneae, spinosae, subrotundae, $100-120\ \mu$ (spinis inclusis), spinis $5-12\ \mu$ obtusis vel acutis.

Hab. AFRICA AUSTRALIS; ad Port Elizabeth *Hodgson* sporas legit, ex quas coluit F. Cavers.

It is only necessary here to supplement Cavers's description of this species by a revised measurement of the spore and a note about the adventitious branching. Spores from herbarium material, from specimens preserved in alcohol and in glycerine jelly, were measured. These gave an average of $109\ \mu$ (including spines). Cavers (1903) gives $80\ \mu$ as an average size. Fig. 8 shows a view of the outer face and fig. 9 of the inner face of a spore. A figure of a plant with stalked adventitious branches (*ad*) is shown in fig. 58. These are similar to those which occur in *R. alatospora* and the *Riella* from Valkenberg vlei. Fig. 58 is made from a specimen in the Manchester Museum mounted in glycerine jelly. The V-shaped structure at the base which is shown here is similar to that described by Cavers as commonly occurring in this species. It suggests that the course of growth has followed the same lines as that of *R. alatospora*, which has been described above.

GENERAL REMARKS ON THE MORPHOLOGY.

The account of the attainment of the adult form, starting with the spore, while not affording any important contribution to our knowledge of the general morphology of *Riella*, is useful in assisting to elucidate some details about which divergent views have been held. The origin of the wing on the spore of *R. alatospora* also calls for comment. The investigation supports Goebel's view that the adult plant in *Riella* is a further development of the primary thallus, and not a new growth on a protonema as suggested by some investigators. One or two secondary intercalary growing points give rise to winged shoots bearing the reproductive organs, and these shoots can live independently if separated from the mother plant. The primary tongue-shaped part of the thallus persisted under favourable conditions in the S. African species examined, although the apical cell ceased to actively divide. It did not decay when the intercalary growing points began to function, as Porsild (1902) and Studhalter (1931) found in their cultures of *R. Paulseni* and *R. americana* respectively.

The formation of twin-shoots, and therefore the maintenance of the bilateral symmetry shown in the primary growth, appears to be more frequent than the study of the literature indicated. That some species are prone to this kind of growth was indicated by the behaviour of *R. alatospora*, which in this respect resembles *R. capensis*.

Apical cell.—Apical cell division occurs in the early stages of growth, but definitely ceases at the tip of the primary body when an intercalary growing point arises. The question whether a single apical cell functions in the intercalary growing region has been disputed. The present work favours Porsild's

(1902) view that a single apical cell is only recognizable in strongly growing plants, and often only at an advanced stage of growth.

The wing of the thallus.—It is now generally accepted that the wing of the shoot bearing the reproductive organs is a dorsal structure. This was maintained by Leitgeb (1879) and Goebel (1907) as opposed to Hofmeister's (1862) suggestion that it is comparable to half the thallus of *Marchantia*. Leitgeb considered the wing to be a comb-like outgrowth of the rib, but he had no young plants showing early stages of growth. Goebel (1907), with young material, showed that the wing-like structure preceded the formation of the rib. Apparently he was here including any part of the thallus which was one-layered after the inception of intercalary growth. The definite wing of the adult shoot is formed almost simultaneously with the rib-tissue, and both are continuous with similar tissues found in the simpler form of thallus preceding this growth.

Scales.—Both rib-tissue and occasionally scales were found in the stalked spathulate structure before the mature winged form of shoot had been produced by the intercalary growing point. The scales in the S. African species are small compared with some of the other species of *Riella*. Trabut (1911) found that in the case of *R. Reuteri* the scales were smaller in submerged forms than in those growing on mud and exposed to the air. In the case of the S. African species plants were not successfully cultivated on mud out of water, so the effect of this change of environment was not proved; there was, however, considerable variation in distribution, size, and form of scale even in a single species grown in water.

Adventitious shoots.—Adventitious shoots, many of which show a simple phase corresponding to the primary thallus of the germ-plant are of frequent occurrence. Probably all species of *Riella* are capable of producing adventitious shoots under certain conditions. In the case of the S. African species described above, when grown under similar conditions in the laboratory it was found that *R. alatospora* was more prone to produce adventitious shoots than *R. purpureospora*. The plants collected from Valkenberg vlei showed the most copious production of adventitious shoots, and these gave a peculiar cauliflower-like form to the plants. Many of these structures were discoid, some with stalks, others sessile. The excessive proliferation shown in this species points to the probability that this occurs under special conditions. A similar but less plentiful branching is shown in a single plant of *R. capensis* in the Manchester Museum collection (see fig. 58). It may be parallel to the gemmiferous condition shown by *R. americana* described by Howe and Underwood (1903) and by the species *R. echinospora* described above (p. 321). The conclusion arrived at is that the plasticity of form shown in the wing, leaf-scales, and branching, together with individual and age differences, often make exact description of the vegetative parts of single plants of little use for purpose of identification.

Wing of the spore.—The wing of the spore in *R. alatospora* is part of a layer (*sw* in fig. 35) which is in process of formation by the four protoplasts before

they have acquired their individual spore-walls (extine and intine). This layer lies just within the mother-cell wall (*mw* in fig. 35) of the tetrad. It forms folds and thickenings along lines which limit laterally the spheres of action of the individual protoplasts. Spines arise from its outer surface, and the thickening of these and other folds give rise to the characteristic garniture of the spore (see figs. 5 & 6). Before this is fully developed the mother-cell wall of the tetrad disappears. Ultimately the individual spores separate, as shown in fig. 36, where two of a tetrad are represented. Meanwhile the individual spores have acquired their two spore coats (extine and intine) shown at *ex* and *in* in fig. 37 which represents a transverse section of a spore of this species. The wing appears to be part of the structure called the perinium, the third coat, present in addition to the extine and intine in the spores of some of the Hepaticae.

Goebel (1893) accepted Leitgeb's view that the perinium is formed from part of the mother-cell of the tetrad. In the case of *Sphaerocarpus*, where the spores usually remain in tetrads up to the time of germination and there is a coat comparable to the perinium of *Riella*, Leitgeb (1879) agreed with Petounikow that the 'special mother-cell wall' persists and forms the patterned outer coat of the tetrad. More recently Lorbeer (1927), investigating the cytology of *Sphaerocarpus Donnellii*, was of the opinion that the gelatinous layer round the spores, in which the garniture of the perinium appears, is built up with the help of the spore mother-cell and neighbouring sterile cells. Siler (1933) has lately reinvestigated the spore-walls of *Sphaerocarpus Donnellii*. She found that the original mother-cell wall of the tetrad usually disappears during the formation of the lining layer which she calls the 'special wall'. She is of the opinion that this is formed by the spore-protoplasts. She says nothing about the function of the sterile cells which accompany the young tetrads in the immature capsule and disappear during the maturation of the spores.

The formation of the perinium in *Riella alatospora* up to the point described above is in agreement with the development of the 'special wall' in *Sphaerocarpus Donnellii* as described by Siler. The continuance of its growth round the inner surface of the spore in *R. alatospora* was not followed.

COMPARISON OF THE SOUTH AFRICAN SPECIES WITH OTHER SPECIES OF RIELLA.

Of all the species of *Riella* which hitherto have been described, only a few show well-marked distinguishing vegetative characters. The large size of the individual and of its scales in the case of *R. Parisii* Gott. is very characteristic, while the tiny creeping form of *R. Reuteri* Mont. distinguishes this from most of the others except *R. Notarisii* Mont., which now seems to have disappeared. *R. bialata* Trab., another tiny form, differs from all the others in the possession of a two-winged thallus.

The other species all bear a general resemblance to *R. helicophylla* Mont., the amount and form of branching proving useful in distinguishing some species if a sufficient amount of material is available.

The form of the involucre and the size, colour, and garniture of the spores appear to offer the most reliable differentiating characters, although there is a certain amount of variation shown even here. Starved plants may produce smaller spores than the average, and the formation of diads instead of tetrads has been noted in some cases.

The four S. African species, *R. capensis* Cavers, *R. purpureospora*, *R. alatospora*, and *R. echinospora*, the species from Grand Canary (*R. affinis* Howe & Underw.), the American species (*R. americana* Howe & Underw.), and one of the N. African species (*R. helicophylla* Mont.) have larger spores than the other known species of *Riella*. *R. helicophylla* occupies an intermediate position; its spores, on the average, are a little smaller than those of the S. African species, and yet are larger than those of the other N. African species and the species represented in Europe and Asia. A tentative key of all the species described up to now is given on pp. 311-12.

Among the species with large spores (100 μ or over) the spores of *R. helicophylla* differ from those of the S. African species in the character of the spines, which are more widely separated and not connected by reticulate thickening in *R. helicophylla*. Moreover they are longer and enlarged at the distal end in this species. Ripe spores of *R. americana* have not been seen by the writer. They are described (Howe & Underwood) as dark brown in colour, having numerous sometimes curved spines (10-24 μ) with dilated apices. The absence of purple colour distinguishes the spores of this species from that of *R. purpureospora*, the absence of wing from those of *R. alatospora*, while the longer spines, sometimes curved and with dilated apices, are unlike the shorter, undilated spines (sometimes acute) of *R. capensis* and the straight more numerous spines of *R. echinospora*. *R. affinis* differs from the S. African species in the character of its involucre, which is winged.

Comparing the S. African forms alone, the involucre of *R. capensis* differs from that of *R. purpureospora* and of *R. alatospora* in its gradual attenuation to a beak instead of a more sudden contraction. The spores have neither the purple colour shown in *R. purpureospora* nor the wing shown in *R. alatospora*; moreover the spines are, on the whole, shorter than in these two species. *R. echinospora* resembles *R. capensis* in the form of its involucre, but the spines on its spores are longer and more numerous, also the reticulations are less well marked in *R. echinospora*. In addition to the colour and the presence of a wing, *R. alatospora* differs from *R. purpureospora* and *R. capensis* in having a stalked involucre; in this last respect it resembles the species from Valkenberg vlei. The stalk and the involucre are, however, more massive in the latter (cf. figs. 1, 4, 7, 10). Also the spores of the plant from Valkenberg vlei show no sign of wings which would have been indicated at the stage shown in fig. 54.

Thus the character of the spore alone suggests that *R. capensis*, *R. purpureospora*, *R. alatospora*, and *R. echinospora* are distinct species. The character

of the involucre offers additional differentiating characters, and distinguishes them from the species from Valkenberg vlei, apart from its peculiar cauliflower-like formation.

Sims (1926, 1927) mentions only one species of *Riella* as occurring in S. Africa. Probably further examination of the plants growing in the pools on the Cape Flats and elsewhere will yield species additional to those now described. Cavers (1903) considered that *R. capensis* was most nearly related to *R. helicophylla*. The vegetative features of *R. alatospora* are very much like those of *R. capensis*, and it was not until the sporogonia ripened that good diagnostic characters were first noted. Both these species frequently show a V-shaped structure at the base, a character shown in other species occasionally, but more characteristic of the plants described by Cavers than the unilateral form of plant. Also stalked adventitious branches (see figs. 28 & 58) were more conspicuous in these two species. The species from Valkenberg vlei showed even greater proliferation, the main stalk being completely hidden by these stalked and sessile structures. Such abundant development of adventitious growths has its analogy in the gemmae described in several other species of *Riella*, amongst which *R. americana* most closely resembles the *Riella* from Valkenberg vlei. The much larger size of the wing and the stalked involucre distinguish this S. African species. Unfortunately the spores were not ripe enough to show colour and ultimate size.

SUMMARY.

1. Three new species of *Riella*—*R. purpureospora*, *R. alatospora*, and *R. echinospora*—and a fourth species lacking ripe spores have been described. These are all native of S. Africa.
2. A diagnosis of *R. capensis* Cavers, involving a revision of the size of the spore, has been given.
3. The early stages of growth and the attainment of the adult form in the three named species have been described, in two of the species from the spore and in the other from the gemma.
4. By their growth form the S. African species constitute a series from a simple or sparingly branched form to a dense shrub-like form.
5. The morphology and relationship of the S. African species has been discussed.
6. A tentative key to all the described species of *Riella* has been provided.

In conclusion, I wish to express my indebtedness to Miss E. L. Stephens for material and notes on the habitats of the new species described in this paper. Thanks are also due to the Director of the Botanical Department at the University of Algiers for M. Trabut's then unpublished descriptions of two of the N. African species of *Riella*—*R. numidica* and *R. sersuensis*—and to the Keeper of Botany at the British Museum for help and access to material in the Herbarium.

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Physiological-ecological investigations in the Wilderness of Judaea. By MICHAEL EVENARI (WALTER SCHWARZ) and RICHARD RICHTER. (Communicated by Dr. ERIC ASHBY, F.L.S.)

(PLATE 23, and, in the text, a map and 23 graphs.)

[Read 11 November 1937]

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AIM AND DESCRIPTION OF THE HABITAT UNDER EXAMINATION.

The work to be described had three aims :—

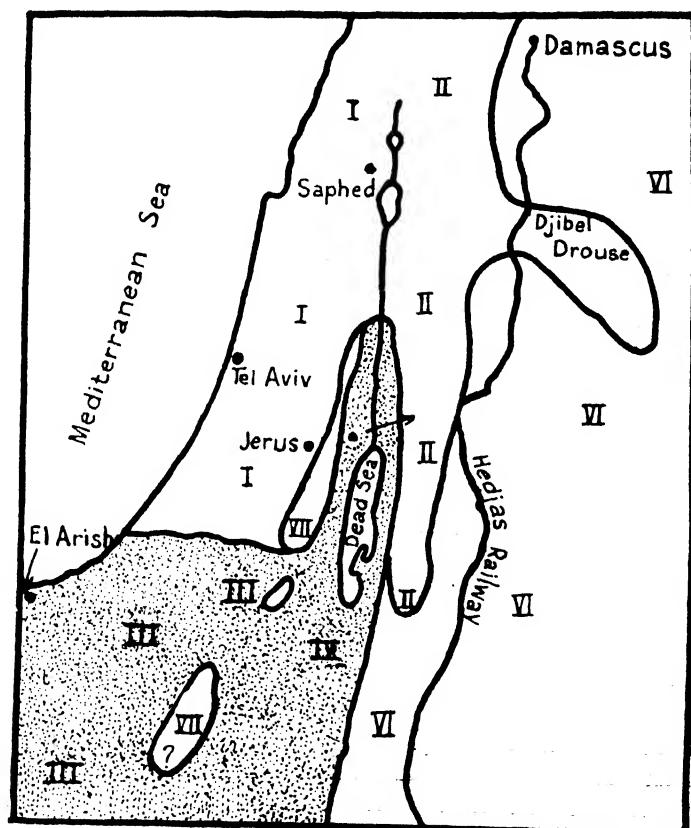
- (1) To observe and compare the water balance of various types of plants in their habitat throughout a complete year.
- (2) To find the effect of external factors on transpiration. The effect of each factor is more obvious in extreme conditions such as those prevailing in the desert.
- (3) To make a contribution to our knowledge of the means by which plants live under extreme desert conditions.

Dates are recorded thus :—20. iii. 34 is the 20th day of March, 1934 ; and hours are recorded as on the 24-hour clock.

The habitat under examination was the desert of Judah, 30 km. wide and 80 km. long, lying to the east and south-east of Jerusalem. It is bounded on the east by the Jordan bed and the west bank of the Dead Sea, and on the west by the mountains of Judah. The habitat is part of the desert belt of south Palestine, Arabia, Sinai, and North Africa. The northern boundary

of the habitat is indefinite, but the desert extends approximately to the junction of the Wadi El Jozole and the Jordan bed, and to the mouth of the Jabrok in the Jordan.

It is a limestone district with deep clefts intersected by deep wadis (dried up river beds) which fall abruptly from about 600 m. above sea-level in the west to about 390 m. below sea-level in the east.



Phyto-geographic sketch of Palestine (after Eig, 1931). I and II, Mediterranean territory ; III and IV, Saharo-Sindian territory ; VI and VII, Irano-Touranian territory. The stations at which investigations were made are indicated by ● →.

The desert of Judah can be divided into two districts :—

- (1) An Irano-Touranian territory in the highest parts.
- (2) A Saharo-Sindian territory.

The major part of the habitat under examination is Saharo-Sindian (Eig, 1931), characterized by (1) extreme dryness of the atmosphere, (2) high tem-



a



b.



c.

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- a. Station I. In the foreground *Suaeda*. On the slopes bushes of *Zygophyllum*.
- b. View from Station II. Looking over the Judaean desert to the North-West. The bushes are *Suaeda asphaltica*. They are densest in the Wadi.
- c. Station II. In the foreground bushes of *Salsola rigida*, in the

perature, (3) slight rainfall, (4) frequent occurrence of salty soils, (5) a paucity of flora both in number and species, (6) monotony of vegetation.

Observations were carried out at two stations:—

Station 1 lies in a wadi-bed, and is situated 29 km. from Jerusalem along the Jerusalem-Kalia Road.

Station 2 is situated on a stony plain 30·5 km. from Jerusalem along the same road. Both are in the Saharo-Sindian territory of the desert of Judah (Pl. 23). A fuller description of plant-distribution and soil-condition, including salt-content, of the two stations will be given in a later paper.

The following is a list of the plants occurring at these stations. The determinations of the plants are according to Eig (1931).—

PLANT-LIST.

Station I.

The names in capitals are those of the plants used in the transpiration experiments. In the second column the biological form is entered. Th.=Therophytes, G=Geophytes, Ph.=Phanerophytes, N.Ph.=Nano-phanerophytes, Ch.=Chamaephytos, H.=Hemicryptophytes. In the third column is denoted what elements the plants represent according to Eig's catalogue: or when such an entry is missing in Eig's catalogue, what Eig calls 'Aire géographique'.

<i>Lamarcchia aurea</i> (Linn.) Moonch.	Th.	Med.-Ir. Tour.
<i>Bromus fasciculatus</i> Presl	Th.	Med.
<i>Muscari commutatum</i> Guss.	G.	Med.
<i>Allium hierochuntinum</i> Boiss.	G.	Sah.-Sind.
<i>Allium Erdelii</i> Zucc.	G	" "
<i>ATRIPLEX HALIMUS</i> Linn.	N.Ph.	Med.
— <i>palaestina</i> Boiss.	"	Sah.-Sind.
<i>SUAEDA ASPHALTICA</i> Boiss.	Ch.	Sah.-Sind.
<i>SALSOLA RIGIDA</i> Pall.	Ch.	Ir.-Tour.
— <i>inermis</i> Forsk.	Th.	Sah.-Sind.
<i>Schanginia baccata</i> Forsk.	Th.	" "
<i>Aizoon hispanicum</i> Linn.	Th.	" "
<i>Mesembrianthemum nodiflorum</i> Linn.	"	Mod.-Sah. Sind.-Trop.
<i>Spergularia diandra</i> (Guss.) Heldr. & Sart.	"	Med.-Ir. Tour.
<i>Spergula flaccida</i> (Roxb.) Aschers.	"	Sah.-Sind.
<i>Silene aegyptiaca</i> (Linn.) Linn. f.	"	Med.
— <i>apetala</i> Willd.	"	Med.-Ir. Tour.
<i>Paronychia capitata</i> Lam.	H.	Med.
<i>Gypsophila Rokejeka</i> Del.	H.	Sah.-Sind.
<i>Pteranthus dichotomus</i> Forsk.	Th.	" "
<i>ERUCARIA BOVEANA</i> Coss.	Th.	" "
<i>Diplotaxis Harra</i> (Forsk.) Boiss.	H.	" "
<i>RESEDA MURICATA</i> Presl	H.	" "
<i>Trigonella arabica</i> Del.	Th.	" "
<i>RETAMA RETAM</i> (Forsk.) Webb	N.Ph.	" "
<i>ERODIUM GLAUCOPHYLLUM</i> Ait.	H.	" "
<i>ZYGOHYLLUM DUMOSUM</i> Boiss.	Ch.	" "
<i>HAPLOHYLLUM TUBERCULATUM</i> (Forsk.) Juss.	H.	Sah. Sind.-Sud. Dec.
<i>Statice Thouini</i> Viv.	Th.	Sah.-Sind.

<i>HELIOTROPIUM ROTUNDIFOLIUM</i> Sieb.	Ch.	Sah.-Sind.
<i>Anchusa aegyptiaca</i> (Linn.) DC.	Th.	" "
<i>Alcanna strigosa</i> Boiss.	H.	Med.
<i>Linaria Haelava</i> (Forsk.) Chav.	Th.	Sah.-Sind.
<i>Cistanche lutea</i> Hoffmigg. & Link	G.	" "
<i>PLANTAGO OVATA</i> Forsk.	Th.	" "
— <i>notata</i> Lag.	"	" "
<i>Asteriscus pygmaeus</i> Coss. & Duv.	"	" "
<i>Senecio coronopifolius</i> Desf.	"	Sah. Sind.-Ir. Tour.
<i>Phagnalon rupestre</i> (Linn.) DC.	Ch.	Med.-Ir. Tour.
<i>Aaronsonia Faktorowskyi</i> Warb. & Eig	Th.	Sah.-Sind.

Station II.

<i>Stipa tortilis</i> Desf.	Th.	Med.-Ir. Tour.-Sah. Sind.
<i>Asphodelus tenuifolius</i> Coss. & Dur.	G.	Sah.-Sind.
<i>BELLEVALIA DESERTORUM</i> Eig & Feinbr.	"	" "
<i>Allium modestum</i> Boiss.	"	" "
<i>ATRIPLEX HALIMUS</i> Linn.	N.Ph.	Med.
<i>SUAEDA ASPHALTICA</i> Boiss.	Ch.	Sah.-Sind.
— <i>vermiculata</i> Forsk.	"	" "
<i>SALSOLA RIGIDA</i> Pall.	"	Ir. Tour.
<i>ANABASIS ARTICULATA</i> (Forsk.) Moq.	"	Sah.-Sind.
<i>Aizoon canariense</i> Linn.	Th.	" "
— <i>hispanicum</i> Linn.	"	" "
<i>Herniaria hemistemon</i> J. Gay	H.	" "
<i>Pteranthus dichotomus</i> Forsk.	Th.	" "
<i>Notoceras bicornue</i> (Ait.) Caruel	Th.	" "
<i>Trigonella stellata</i> Forsk.	Th.	" "
<i>Astragalus tribuloides</i> Del.	Th.	" "
<i>Lotus peregrinus</i> Linn. var. <i>brachypodus</i> Oppenheimer	Th.	Sah. Sind.-Ir. Tour.
<i>Euphorbia Chamaepeplus</i> Boiss. & Gaill. var. <i>sinaica</i> Boiss.	Th.
<i>Reaumuria palustrina</i> Boiss.	Ch.	Sah.-Sind.
<i>Statice Thouini</i> Viv.	Th.	" "
<i>Arnebia decumbens</i> (Vert.) Coss. & Kralik	Th.	Sah. Sind.-Ir. Tour.
<i>Echium plantagineum</i> Linn.	Th.	Med.
<i>Linaria Haelava</i> (Forsk.) Chav.	Th.	Sah.-Sind.
<i>Plantago ovata</i> Forsk.	Th.	" "
— <i>notata</i> Lag.	Th.	Ir. Tour.-Sah. Sind.
<i>Urospermum picroides</i> (Linn.) Schmidt	Th.	Med.-Ir. Tour.
<i>Asteriscus pygmaeus</i> Coss. & Dur.	Th.	Sah.-Sind.
<i>Actractylis cancellata</i> Linn.	Th.	Med.

MACRO-CLIMATE OF THE JUDAean DESERT.

Rainfall.—The average annual rainfall of Jericho in the Judaean desert is 106 mm. The months January and February have the heaviest rainfall ; May-September, no rain ; other months, slight rain. The annual amount of rainfall gives insufficient information. Distribution and fluctuation of annual rainfall is of the greatest importance to plant-life.

The following examples show the fluctuations in the annual rainfall :—In the year 1930, 159·5 mm. In the year 1932, 54·5 mm.

The length of summer drought varies :—In 1928 there were seven rainless months. In 1930 four rainless months.

The rainfall in a particular month shows great variation :—In December 1930, 3·5 mm. : in December 1933, 49·0 mm.

The beginning of rain is not constant :—In 1926 rain began in December : in 1931 rain began in October : in 1932 rain began in October.

The number of days in the year with more than 1 mm. rainfall varies :—In 1930–31, 23 days : in 1931–32, 16 days : in 1932–33, 17 days.

Comparison with other desert regions.—The following figures show :—

(1) Great contrasts of rainfall in the small area of Palestine ; (2) that the rainfall in the Judaean desert, like that of Repetek in the sand-desert of Kara-Kum, has a medium value.

Annual rainfall of towns in Palestine : Jerusalem 663 mm. : Metullah 975 mm.

Annual rainfall in desert regions :—En Nachl 0·25 mm. : Helouan 34 mm. : Repetek 102 mm. : Jericho 106 mm. : Biskra 174 mm. : Tucson 302 mm.

Beni-Ounif (Algerian Sahara) has the same annual rainfall as Jericho, but has no rainless month. North American desert has no rainless month and has both a winter and a summer maximum rainfall. Helouan (1904–24) had an average of 6·5 days per season with an average of more than 1 mm. rainfall.

Temperature.—The average annual temperature of Jericho is 23·1° C. ; and a temperature of 45° C. is reached or exceeded every year. Between 1919 and 1926 the maximum temperature was 47° C., the minimum 2·2° C.

Comparison with other desert regions.—The average yearly temperature of Helouan is 21·2° C. and of Repetek 17·0° C. At Helouan between 1919 and 1926 a temperature exceeding 43° C. was reached in only four out of the eight years. The maximum temperature reached was 46·3° C. and the minimum 1·6° C.

Relative humidity and saturation-deficit. Saturation-deficit is of greatest importance during transpiration-measurement. The relative humidity of Jericho is 51 per cent. ; the average annual saturation-deficit is 11·64 mm.

Comparison with other regions.—Helouan has a relative humidity of 50 per cent. and a saturation-deficit of 11·7 mm.

Evaporation.—The annual evaporation in Jericho is 3038·0 cubic centimetres. The quotient $\frac{\text{annual evaporation}}{\text{annual rainfall}}$ = 28·6. This quotient is important in the study of plant-life and soil-investigation (e.g. salt content).

Comparison with other regions. Jerusalem, annual evaporation = 1873.7 cubic cm., quotient $\frac{\text{annual evaporation}}{\text{annual rainfall}}$ = 2.83.

Helouan annual evaporation = 2395.0 cubic cm.,

$$\text{quotient } \frac{\text{annual evaporation}}{\text{annual rainfall}} = 70.5.$$

In northern climates, e.g. Leningrad, the quotient is less than 1.

Wind.—The average annual velocity of the wind is small, being 1.7 m. per second; and fluctuations in this value are also small, varying from 1.2 m. per second in October to approximately 2.1 m. in April.

In Helouan the average annual velocity of the wind is 4.8 m. per second. Two winds, the *Chamssine* and a *Foehn*-like wind, have a great effect on the Judaean desert. The *Chamssine* is a hot easterly wind which greatly increases temperature, evaporation, and the saturation-deficit of the atmosphere. If these winds occur when the soil begins to dry (end of April to mid-May) they are a limiting factor for the vegetation, especially of annuals; but if they occur in early spring, when the soil is well watered, they have a stimulating effect on all vegetation. The *Foehn* is a hot dry westerly wind, occurring in summer, and causing temperature and saturation-deficit to rise to a second maximum after 16 o'clock or 4 p.m.

This wind is a Mediterranean sea-breeze occurring in mid-day, and in passing over the desert it becomes hot and dry. It is adiabatically heated during its fall of 1200 m. from Jerusalem to the Dead Sea (Ashbell, 1934).

METHOD OF EXPERIMENT.

Transpiration measurements were made on cut branches or leaves using Huber's method (1927; see also Pfleiderer, 1933). The organs were removed, weighed, exposed for two minutes, and then re-weighed. Cutting under paraffin proved to be unnecessary. The following precautions were taken:—(1) the time for cutting and weighing was reduced to a few seconds; (2) the several organs were exposed in a similar position to that in which they were growing, since small alterations in position and height caused variation in the amount of transpiration. With a two minutes' exposure, little variation was found in the results obtained from neighbouring branches cut at the same time; (3) the balance was protected from the wind by a special box.

The surface of the organs was measured by tracing. The dry weight of the severed organs was found in the laboratory, the material being heated in a drying oven to a temperature of 105° C.

In the case of *Suaeda*, *Zygophyllum*, and *Salsola* difficulty was experienced in making surface-measurements. These difficulties could not be overcome in the case of *Salsola*. The following method was adopted in the case of *Suaeda* and *Zygophyllum*. For each series of readings two specimens were obtained at the same time and place. Of one specimen the fresh weight and the surface

measurement were found, the latter with the help of a microscope. Of the second specimen the ratio $\frac{\text{fresh weight}}{\text{dry weight}}$ was found. Since this ratio was the same for both specimens and proved to be nearly constant within one day, the ratio $\frac{\text{surface}}{\text{dry weight}}$ and therefore surface was obtainable for any specimen.

The following quotients were established, area being measured in square decimetres, weight and water-content in grammes, transpiration in milligrammes :—

$$\frac{\text{surface}}{\text{dry weight}}, \quad \frac{\text{surface}}{\text{fresh weight}}, \quad \frac{\text{water-content}}{\text{surface}}, \quad \frac{\text{water-content}}{\text{dry weight}}.$$

We did not use Stocker's method (1929 *a* and *c*) for the establishment of the saturation-deficit as it was not possible to measure the water-saturation of the cut organs at the habitat. It seemed too long before we could place them in water in the laboratory for the readings to be of any use. We used Wassiljiew's method (1937).

The difference between the smallest and largest water-content (per 100 gm. dry weight) in relation to the highest water-content taken as 100 gives the daily maximum fluctuations of the water-saturation-deficit. Hourly readings were taken from before sunrise until night-fall. Some readings were taken during the night.

These figures do not tell anything about the difference between the absolute water-saturation under optimal and minimal conditions (Welten, 1933). We cannot assume that the water-content taken before sunrise in the dry season can be compared with the maximum possible water-content measured by Stocker's method. Proof of this is the fall of the quotient $\frac{\text{water-content}}{\text{dry weight}}$ during the dry season (see Table V). This means that the daily water-deficit in the dry season cannot be entirely recovered by the plant over night. The morning water-content-deficit (Welten, 1933), which we call the latent water-saturation-deficit, can be verified by reference to the maximum water-content possible in the year.

Suction-pressure of the soil was measured according to Hansen's method simplified by Stocker (1930), a solution of common salt replacing the sugar in the filtration papers. *Evaporation* was measured partly by Piche's evaporimeter and partly by Stocker's method (1929 *b*). In the second method green discs of filter-paper were exposed for two minutes between two weighings as in the case of the plant-organs. This method gave better results on days with variable cloud, wind, and temperature conditions. Piche's evaporimeter did not record the small changes, which are of great importance to transpiration. With uniform meteorological conditions no difference was observed in the evaporation-curves obtained by the two methods. *Atmospheric moisture* was measured with the wet and dry swing thermometer; *temperature of the*

soil with a soil thermometer; *light intensity* with a photometer according to the method of Eder-Hecht and *velocity of wind* with an anemometer. *The overcasting of the sun* was estimated with the help of the Scala S_0-S_4 in five parts

TABLE I.—*Water-content and soil suction-pressure.*

	Date.	Position.	Depth.	Water-content as per cent. of fresh weight.	Suction- pressure in mol. NaCl.
<i>Station 1.</i>					
I a.	14. ii. 34.	Middle of wadi.	Surface.	13.05	0.33
	"	"	25 cm.	13.25	0.31
	"	Southern slope.	Surface.	5.78	0.7
	"	Northern slope.	"	9.25	0.45
I b.	20. iii. 34.	Middle of wadi.	Surface.	1.56	>4
	"	"	5-10 cm.	6.70	0.6-0.7
	"	"	40-50 cm.	8.64	0.4-0.5
I c.	30. v. 34.	Middle of wadi.	Surface.	>4
	"	"	20-30 cm.	5.88	1.4-1.5
	"	"	30-40 cm.	6.20	1.1-1.2
I d.	26. vi. 34.	Middle of wadi.	Surface.	>4
	"	"	20-30 cm.	3.5-3.7
	"	"	50-60 cm.	5.83	1.4-1.5
I e.	4. viii. 34.	Middle of wadi.	Surface.	2.75	>4
	"	"	20-30 cm.	3.4	>4
	"	"	30-40 cm.	4.6	>4
I f.	24. xi. 34.	Dry plac.	Surface.	4.9	2.5
	"	"	20 cm.	6.0	2.0
	"	"	40 cm.	6.4	1.4-1.5
	"	"	70 cm.	7.6	1.3-1.4
	Wet plac.	Surface.	19.1	1.25-1.3	
			21.0	1.25-1.3	
			19.4	1.2-1.3	
<i>Station 2.</i>					
I g.	18. i. 34.	Southern slope.	Surface.	19.2
	"	"	35 cm.	4.6
	"	Middle of wadi.	Surface.	25.4
	"	"	35 cm.	20.8
	"	Northern slope.	30 cm.	16.7

and the overcasting of the whole sky by the Scala B_0-B_9 in ten parts. *The measurement of the width of the stomata* was obtained by the infiltration method, using xylol, alcohol, oleum terebinthi, and petroleum.

No results were obtained in the case of *Salsola* owing to the shape and smallness of the leaves, nor in the case of *Retama* owing to the position of the stomata in the hairy groove of the stem. We do not understand how Firbas (1931 b), using the infiltration-method, obtained figures in the case of *Retama*.

TABLE II.—*Evaporation according to Piche on 30/31. v. 34
and soil and air temperature on 30/31. v. 34.*

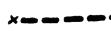
Time.	Evaporation in cubic cm.	Temperature in degrees C.		
		Soil.		Air temperature.
		Surface.	Depth of 15 cm.	
9.30-10.30	1.3	40°.8 C.	29° C.	31° C.
10.30-11.30	1.45
11.30-12.30	1.75	48	29.8	32
12.30-13.30	1.6	48.5	31	33
13.30-14.30	1.5	46	31	33
14.30-15.30	1.3
15.30-16.30	1.2	44	32	32
16.30-17.30	1.0
17.30-18.30	0.8	37.2	32.3	29
18.30-20.30	1.6	32.2	32.5	25
20.30-2.00	1.8
2.00-3.30	0.6	21	30	20.2
3.30-4.30	0.2
4.30-5.30	0.2	20.5	29.5	21
5.30-6.30	0.3
6.30-7.30	0.7	25	28.9	24.5
7.30-8.30	0.75	30.5	28.8	26.5
8.30-9.30	0.85	41	29	30.5
Total	18.90			

Transpiration experiments.—As an example of the type of observations we carried out we give the details of one day's results (see also tabulated results, Tables XIV and XV):—

30-31 May, 1934. *Station 1.*

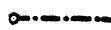
Since the beginning of the rainy season 94.5 mm. of rain had fallen. All annuals were dead. *Suaeda* bore ripe seeds and dried up leaves, light red in colour, resembling the autumn tints of deciduous trees. The young shoots of *Retama* were already woody and the plants bore ripe seeds. *Haplophyllum* and *Heliotropium* were in flower. *Erodium* plants bore ripe fruits and covered a large surface of the ground. The leaves had many holes, and were obviously about to wither. *Reseda* had ceased flowering, but its green leaves were in

A key to the lines and signs in the following graphs.

 = atmospheric evaporation,

 = atmospheric water-saturation deficit,

 = transpiration of *Retama*,

 = transpiration of *Salsola*,

 = transpiration of *Haplophyllum*,

 = transpiration of *Heliotropium*,

 = transpiration of *Reseda*,

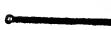
 = transpiration of *Zygophyllum*,

 = transpiration of *Erodium*,

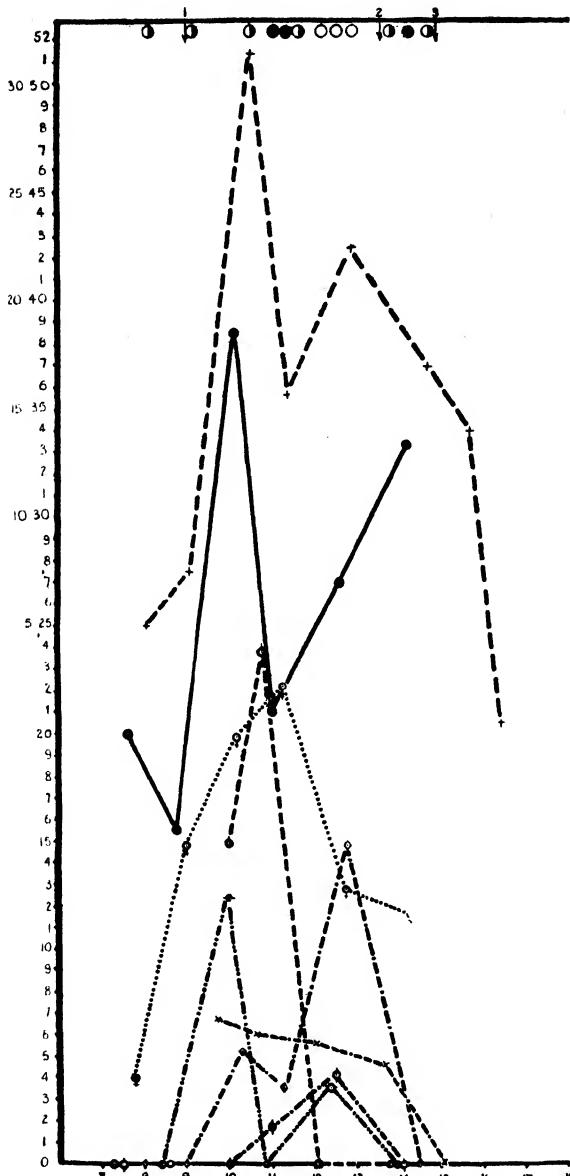
 = transpiration of *Suaeda*,

 = transpiration of *Atriplex*,

 = surface transpiration of *Anabasis*,

 = fresh-weight transpiration of *Anabasis*,

 = water-content transpiration of *Anabasis*.



GRAPH 1.—Fresh-weight transpiration and evaporation on 3.i.34. Scale: transpiration, 0-52 mg./g./min.; evaporation, 0-30 mg./min. (↓) Sunrise for *Retama*. (↑) Sunset for *Heliotropium*. (§) Sunset for *Suaeda*.

good condition. *Zygophyllum* plants bore ripe fruits and most of the leaves had fallen. They lay in heaps at the base of each plant, and it was clear that they turn yellow, dry completely on the bush, and then fall, the petioles remaining on the bush.

The day was windless until the beginning of the Chamssine in the afternoon and sunshine was continuous throughout the day. Soil and air temperatures taken in the middle of the wadi are recorded in Table II. It is interesting to note that although sunrise occurred at 4.30 a.m., the surface temperature did not exceed the atmospheric temperature until 6.30 a.m. The maximum atmospheric temperature was 33° C. at 13.30 o'clock, and at this time the temperature at the surface was 46° C.

Water-saturation-deficit falls to a minimum of 7.4 mm. a few minutes before sunrise, after which it rises rapidly. Maximum relative humidity is reached shortly after sunrise and is 62 per cent., and its value during the day does not exceed 30 per cent. until 18 o'clock.

Soil water and soil suction-pressure results are recorded in Table I c (p. 340). It may be noted that the soil suction-pressure does not fall below one mol. sodium chloride even at a depth of 30 to 50 cm.

Atmospheric evaporation measured according to Piche is recorded in Table II. Between 17.30 p.m. and 4.30 a.m. the total amount of evaporation was 5.0 cubic cm. and during the rest of the 24 hours it was 13.9 cubic cm., rising to a maximum of 1.75 cubic cm. per hour between 11.30 and 12.30.

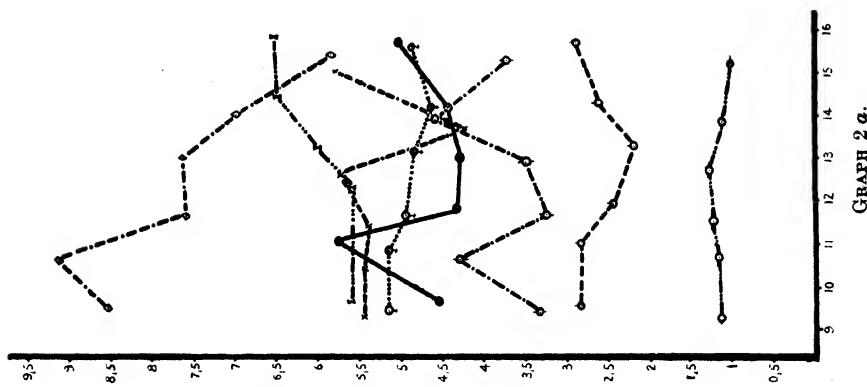
DISCUSSION.

(1) Daily course of the transpiration curves.

The data for transpiration are presented in graphs 1-12.

(A) *Course of transpiration*.—The curves can be divided into single apex, double apex, and triple apex curves. Further, they can be grouped into (1) curves parallel to those of evaporation and water-saturation-deficit, here both single and double apex curves occur; (2) curves not parallel to evaporation and water-saturation-deficit, here double and triple apex curves occur. This parallelism of the curves (graph 1, on 3. i. 34, and graph 8, on 24. xi. 34) is only observable when the soil has a high water-content. On the first experimental day after the first rainfall of the season (24. xi. 34) a great number of transpiration curves run parallel to those of evaporation and water-saturation-deficit for the first time since 20. iii. 34. Non-parallelism is practically confined to those days when the soil-water-content is poor (graphs 3, 3 a, on 20. iii. 34). The curves show two prominent exceptions, *Reseda* in which the maximum transpiration coincides with the minimum evaporation (graph 1, 3. i. 34) and *Salsola* (graph 3, 20. iii. 34). On this day the *Salsola*-curve alone was parallel to that showing evaporation and water-saturation-deficit.

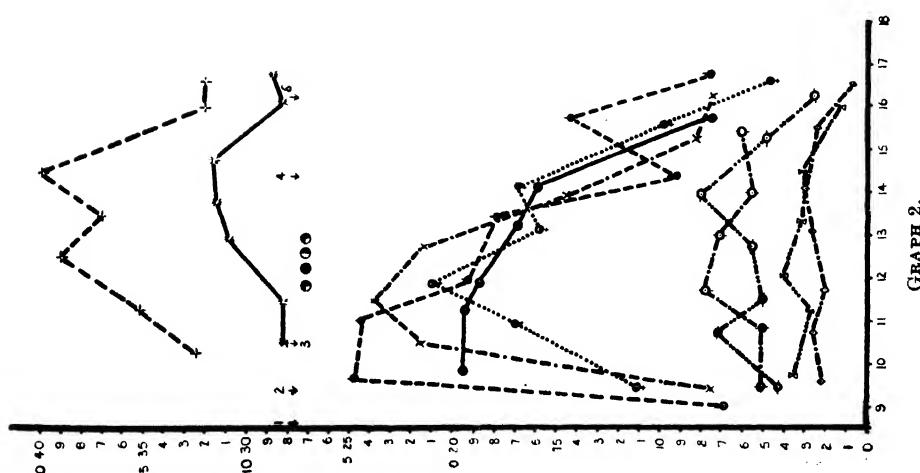
Whereas single apex and double apex curves have long been known (Stocker, 1935), the regular triple-apex curves were observed for the first



GRAPH 2. — Fresh-weight transpiration, evaporation, and water-saturation deficit of the atmosphere on 14. ii. 34. Scale : transpiration, 0-40 mg./g./min.; evaporation, 0-20 mg./min.; saturation deficit in mm.

(1) First rays of the sun strike the wadi.
 (2) Sunrise for *Heliotropium*.
 (3) Sun-rise for *Rzedea*.
 (4) Sunset for *Erodium*.
 (5) The last rays of the sun strike the wadi.

GRAPH 2 a.— Water-content on
14. ii. 34.



GRAPH 2 a.

time and seem to be a specific feature of desert transpiration. The main characteristics are: first fall between 7 and 10 a.m., second rise at midday, third rise in the afternoon (*Heliotropium*, graph 6, p. 352).

(B) *Factors affecting the daily course of transpiration curves.*—The following factors are found to play a part :—

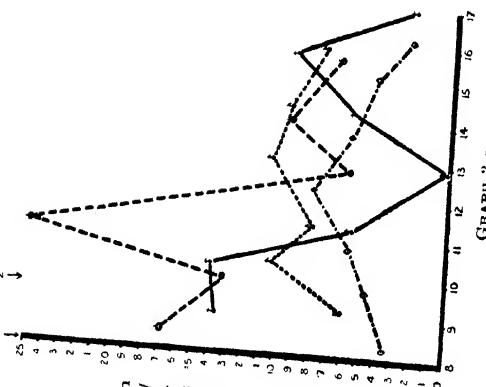
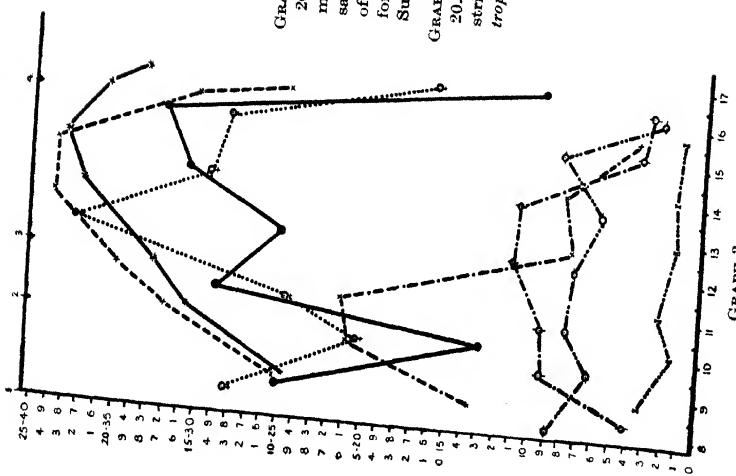
- (1) Suction-pressure of the soil.
- (2) Evaporating power of the atmosphere.
- (3) Water-condition of the plant (hydratur, Walter, 1931).
- (4) Stomatal movement.
- (5) Wind.

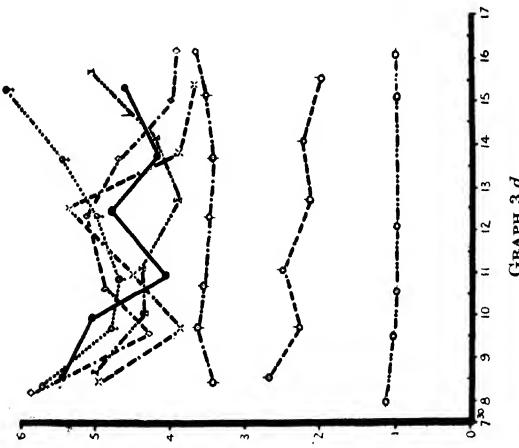
When the transpiration-curves run parallel to those of evaporation and water-saturation-deficit, factors (1), (2), and (3) are the most important. (1) Parallelism occurs on days with low suction-pressure. If the suction-pressure rises (as from 20. iii. 34, graph 3, 3 a, to 29. ix. 34, graph 7), parallelism ceases. (2) If on a day with low suction-pressure in consequence of a Chamssine, the evaporation is very big, the parallelism ceases and counter-running curves are observed. But a high suction-pressure appears to have more effect on the parallelism of transpiration and evaporation and water-saturation-deficit curves than evaporation. This is shown by graphs 3, 3 a, and 7 (pp. 347 & 353), all of which show the same evaporation of 8.7 cm. per day (Piche), but which vary greatly as to suction-pressure. (3) The effect of the water-condition of the plant was not determined exactly, since no measurements of osmotic pressure were made. Yet the quotient $\frac{\text{water-content}}{\text{dry weight}}$ (graph 13, p. 366), gives a good measure of the water-condition of the plant, provided that measurements are made on the same plant. When the $\frac{\text{water-content}}{\text{dry weight}}$ value falls the parallelism decreases and the reverse. The water-content of the plant is obviously dependent upon factors 1 and 2, above.

It is interesting to note that the parallelism of the curves *evaporation*, *water-saturation-deficit* and *fresh-weight transpiration* ceases in the various plants at different times of the year.

The following examples seem to be of importance with regard to the recognition of the transpiration conditions of the various species. On 3. i. 34, graph 1 (p. 343), the curve of *Reseda* is non-parallel. On 14. ii. 34, graph 2 (p. 345), this occurs in the case of *Heliotropium*, whereas all other plants show parallelism, while on 20. iii. 34, graph 3 (p. 347), the curve of *Salsola* alone shows parallelism, and on 24. xi. 34, graph 8 (p. 354), all curves show parallelism except those of *Haplophyllum* and *Suaeda*.

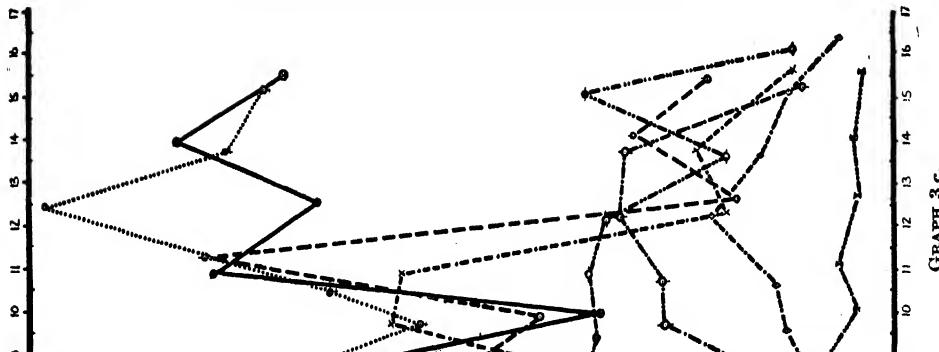
(4) *Stomata.* Apart from the saturation-deficit of the atmosphere, our investigation shows that the most important factor influencing the transpiration is the movement of the stomata. Nearly all the large fluctuations



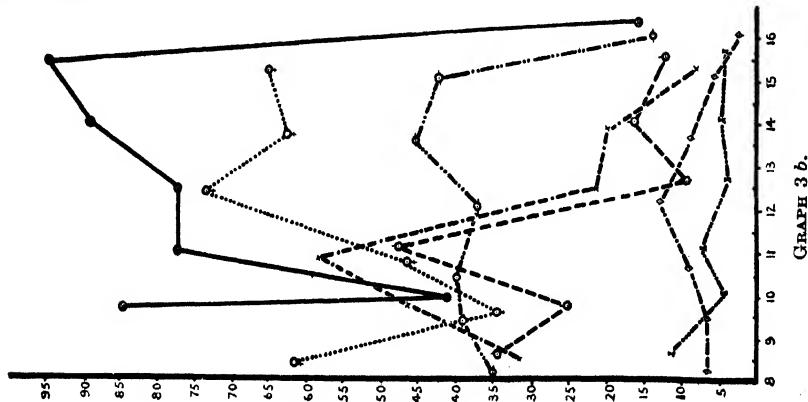


GRAPH 3 b.—Surface transpiration on 20. iii. 34. Scale, 0–95 mg./dm.²/min.
GRAPH 3 c.—Water-content transpiration curves, 20. iii. 34.

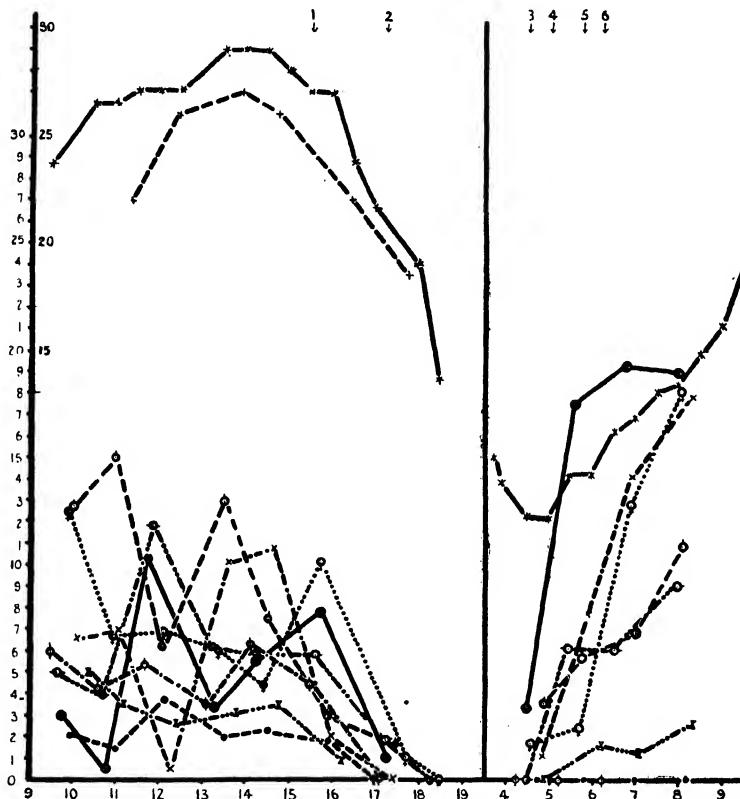
GRAPH 3 d.— $\frac{\text{Water-content}}{\text{Dry weight}}$ quotient on



GRAPH 3 C



of the transpiration curves are accompanied by opening or closing of the stomata, but this is not so in the case of small fluctuations. In those cases where the *fresh-weight transpiration* and *water-content transpiration* results vary greatly from those of *surface transpiration*, the results may be related to the movements of the stomata. Although it is difficult to dissociate light and temperature effects, light intensity is of first importance in the consideration

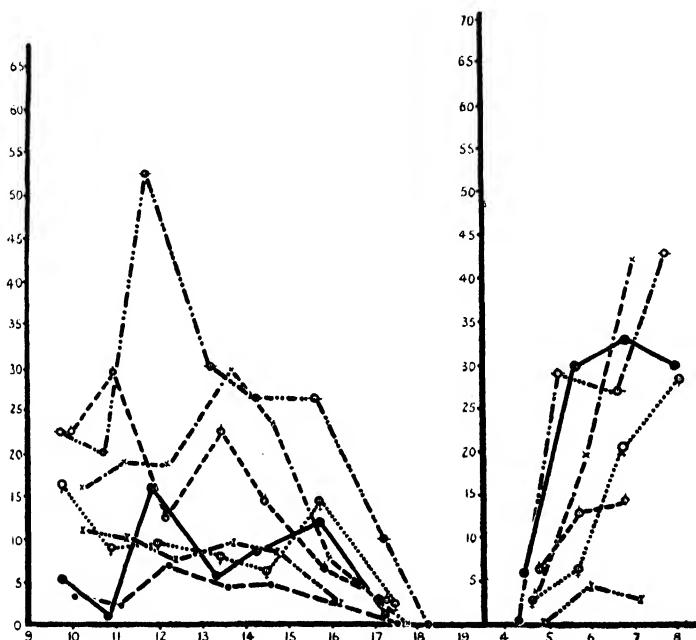


GRAPH 4.—Fresh-weight transpiration, evaporation, and water-saturation deficit on 30/31. v. 34. Scale : transpiration, 0-30 mg./g./min.; evaporation, 15-30 mg./min.; water-saturation deficit in mm. (↓) Sunset for *Heliotropium*, *Erodium*, and *Zygophyllum*. (‡) All plants in the shade. (§) First rays of the sun strike the wadi. (¶) Sunrise for all plants except *Zygophyllum* and *Reseda*. (¤) Sunrise for *Zygophyllum*. (¤) Sunrise for *Reseda*.

of the movement of the stomata. Usually the stomata open and transpiration rises higher than evaporation when the direct rays of the sun reach the organs of the plant; also the stomata begin to close as soon as the plants are in the shade. The important factor is direct sunlight and not diffused light. Good

examples of this fact are shown in graph 4 (p. 349), where the early fall in the transpiration curve of *Heliotropium* and the late rise in the curve for *Zygophyllum* and *Reseda* are entirely caused by the time at which the last and first rays of the sun touch the plants. In the morning, the stomata of all plants, especially *Heliotropium*, *Haplophyllum*, *Reseda*, and *Erodium* open quickly, but they close slowly in the evening. It was not clear how to account for this.

An exception occurred in the case of young *Heliotropium*, 30–31. v. 34 graph 4, where the transpiration, though it fell on the cessation of direct sunlight, did not cease entirely nor did the stomata close for some considerable

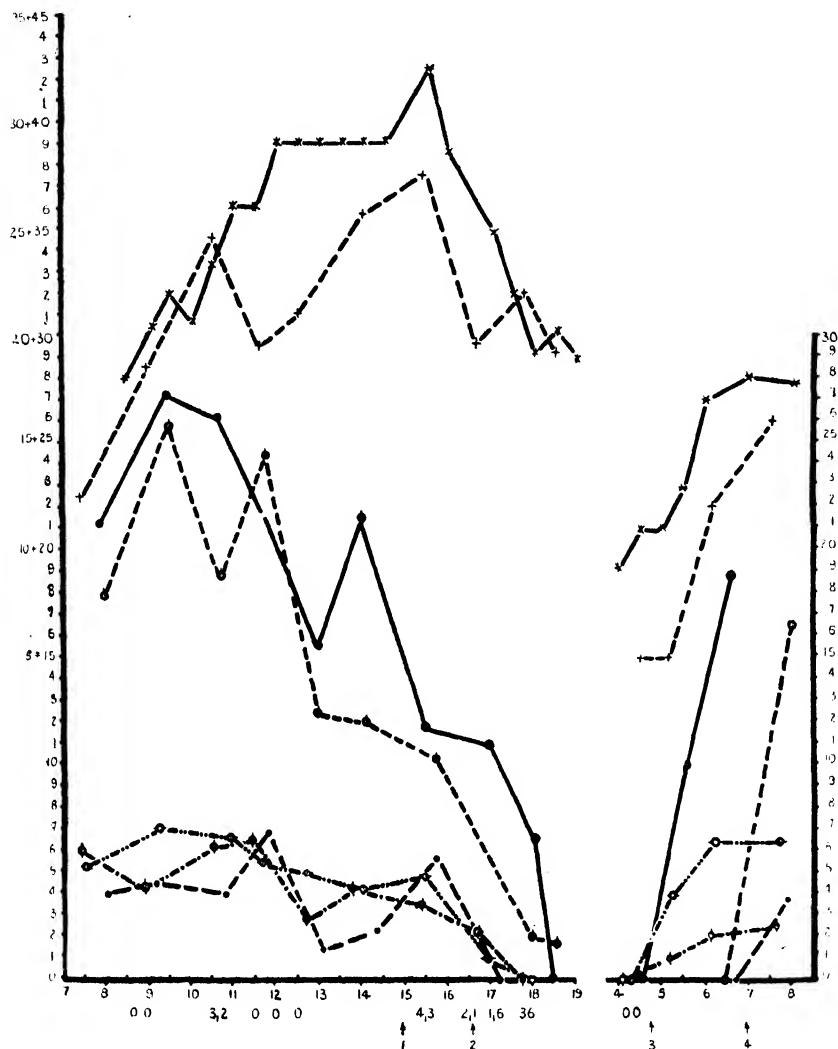


GRAPH 4 a.—Surface transpiration on 30/31. v. 34.

time after dark. The further proof of the sensitiveness of the stomatal apparatus to direct as opposed to diffused sunlight is its behaviour when the sun is suddenly overcast. Sudden overcasting of the sun caused an almost instantaneous fall in transpiration and closing, sometimes complete, of the stomata—graph 1 (p. 343), *Retama*, *Haplophyllum*, and *Heliotropium*: graph 2 (p. 345), *Retama*, *Heliotropium*, and *Suaeda*.

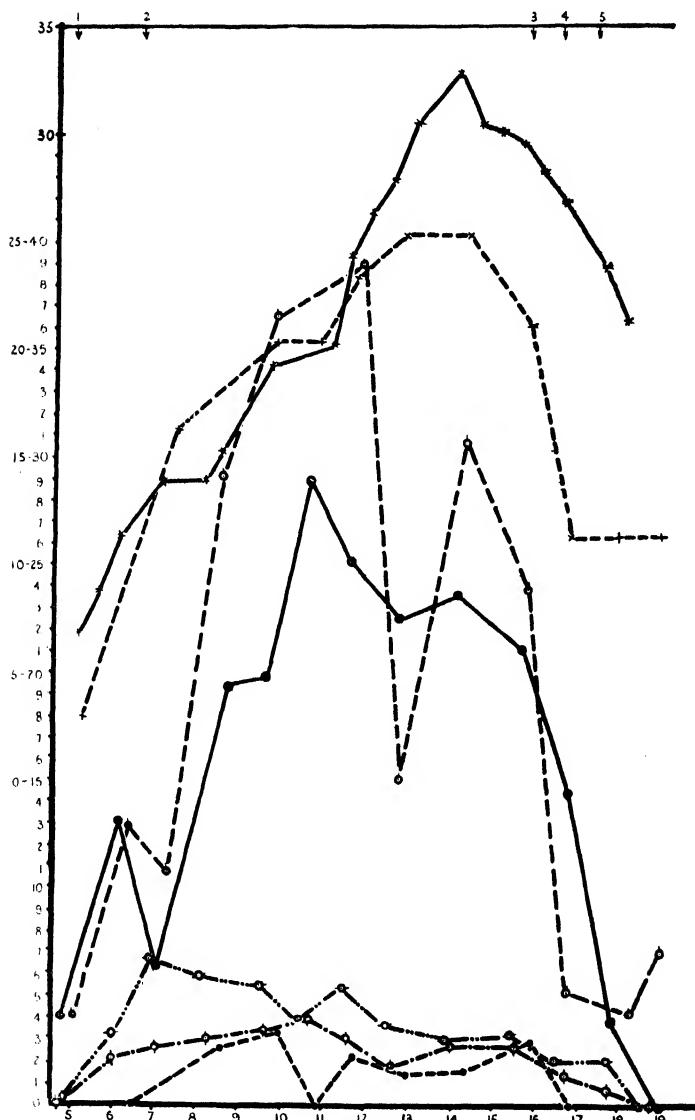
All plants do not react in exactly the same way, and also the same plant at different times may show a varying response to the light-stimulus. Amongst the plants investigated, *Heliotropium* reacted best to varying light-conditions, while *Zygophyllum*, *Suaeda*, and *Salsola* reacted least.

On cloudless days, when there is no fluctuation in the light intensity and when the suction-pressure of the soil is high, the transpiration curves do not

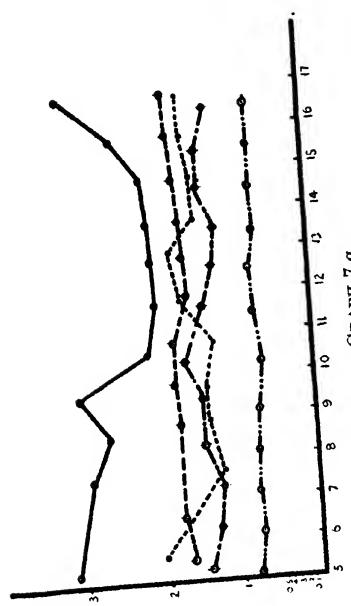


GRAPH 5.—Fresh-weight transpiration, evaporation, and water-saturation deficit on 26/27. vi. 34. Scale : transpiration, 0-45 mg./g./min.; evaporation, 0-35 mg./min.; water-saturation deficit in mm. The force of the wind is noted below the scale of time. (\uparrow) Sunset and the beginning of the hot west wind (Table XIV). (\uparrow) Sunrise for *Salsola*, *Retama*, and *Haplophyllum*. (\uparrow) Sunrise for *Heliotropium* and *Atriplex*.

show parallelism with those of evaporation and water-saturation-deficit. The maxima and minima of the triple and double apex curves depend here upon

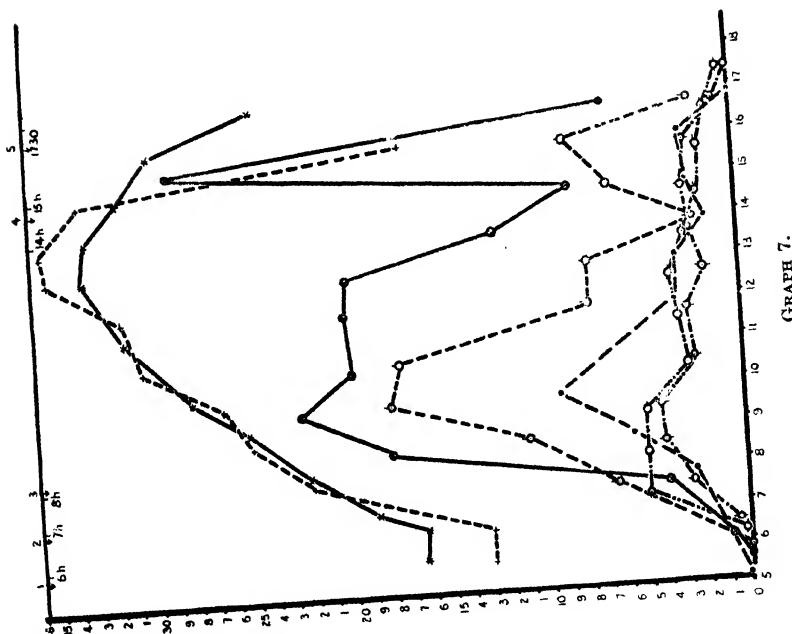


GRAPH 6.—Fresh-weight transpiration, evaporation, and water-saturation deficit on 4. viii. 34. Scale: transpiration, 0-40 mg./g./min.; evaporation, 0-35 mg./min.; water-saturation deficit in mm. (↓) Sunrise for all plants except *Atriplex*. (↑) Sunrise for *Atriplex*. (↑) Sunset for *Atriplex* and *Heliotropium*. (↑) Sunset for *Haplophyllum*. (↑) Last rays of the sun strike the wadi.

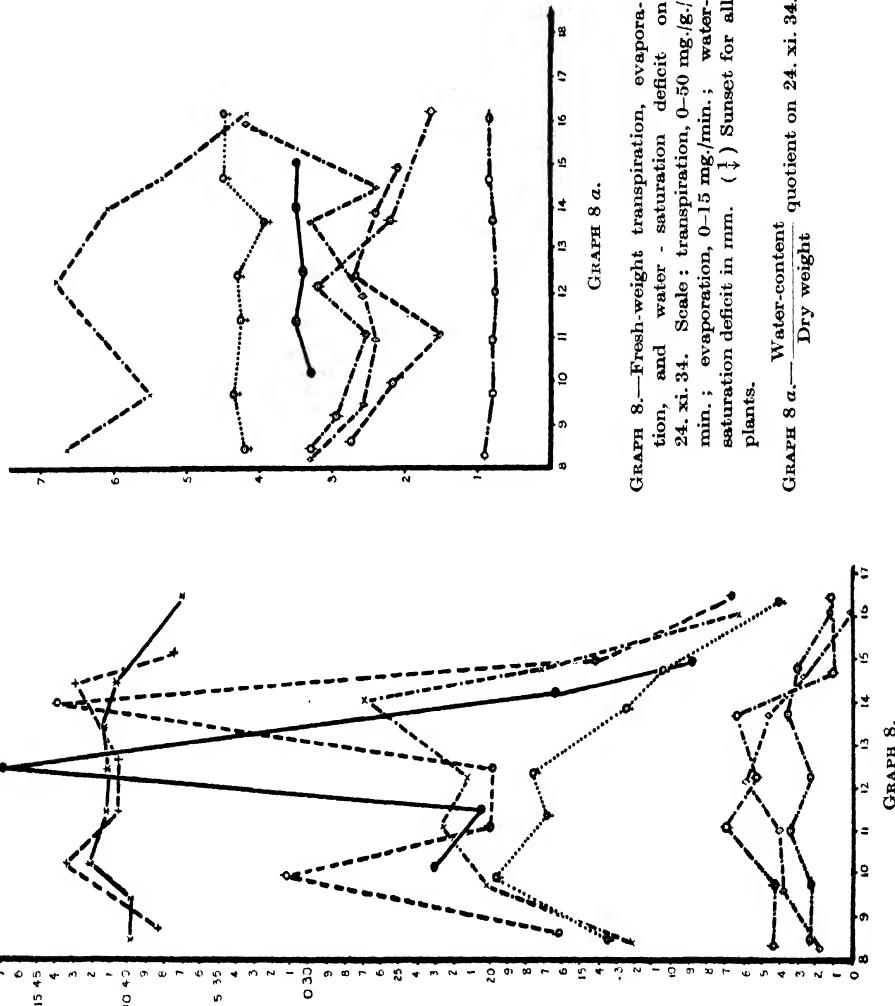


GRAPH 7.—Fresh-weight transpiration, evaporation, and water-saturation deficit on 29. ix. 34. Scale : transpiration, evaporation 0-36 mg./min.; water-saturation deficit in mm. (1) First rays of the sun strike 0-36 mg./min.; evaporation 0-36 mg./min.; water-saturation deficit in mm. (2) Sunrise for *Atriplex*, *Haplophyllum*, and the wadi. (3) Sunrise for *Salsola*. (4) Sunset for *Heliotropium*. (5) Last rays of the sun strike *Atriplex* and *Salsola*. (6) Last rays of the sun strike the wadi: sunset for *Heliotropium* and *Haplophyllum*.

GRAPH 7 a.—Water-content quotient on 29. ix. 34.
GRAPH 7 a.—Dry weight



the movements of the stomata. Movements of the stomata can only be accounted for by the hydroactive closing movement being followed by a photo-active opening movement (Stalfelt, 1932, p. 24). The beginning of the closing movement will depend upon the water-condition of each individual plant.



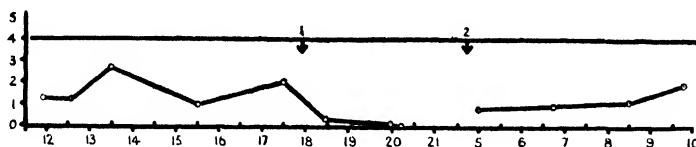
GRAPH 8.—Fresh-weight transpiration, evaporation, and water-saturation deficit on 24. xi. 34. Scale : transpiration, 0-50 mg./g./min.; evaporation, 0-15 mg./min.; water-saturation deficit in mm. (↑) Sunset for all plants.

GRAPH 8 a.— $\frac{\text{Water-content}}{\text{Dry weight}}$ quotient on 24. xi. 34.

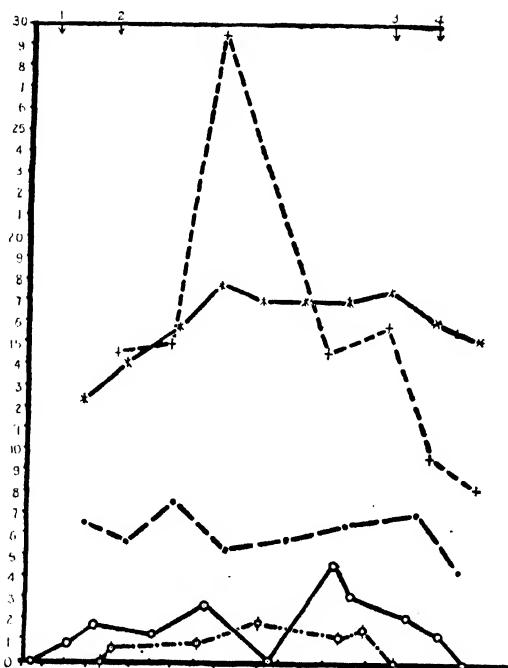
(5) Wind. It is usual to find an influence of wind upon evaporation, water-saturation-deficit, and transpiration by studying the influence of strong winds : but in the Judaean desert the variations in the velocity of the wind are usually very small. When strong winds do occur, they are so hot that they affect the temperature to such an extent that it is not possible to separate the effects

of wind and temperature. We have therefore observed the influence of lack of wind on transpiration.

It is interesting to note the unequal reactions of evaporation and water-saturation-deficit to alterations in the meteorological factors. On 14. ii. 34,



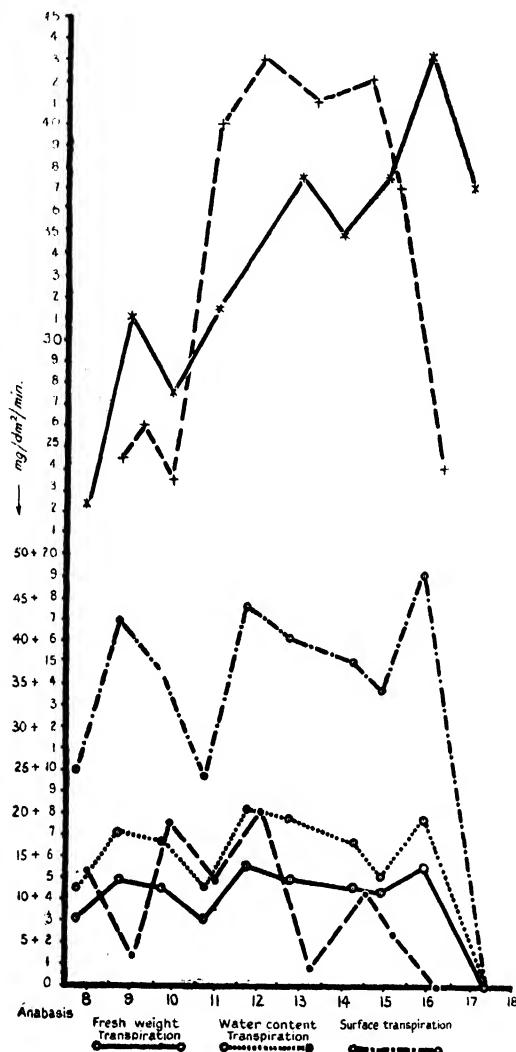
GRAPH 9.—Fresh-weight transpiration on 9/10.viii.33 of *Anabasis*. Scale 0-5 mg./g./min. Scale of time : 12-21 on 9. viii. 33 ; 5-10 on 10. viii. 33. (1) Sunset for all plants. (2) Sunrise for all plants.



GRAPH 10.—Fresh-weight transpiration, evaporation, and water saturation deficit on 20. xi. 33. Scale : transpiration, 0-30 mg./g./min.; evaporation, 0-30 mg./min.; water-saturation deficit in mm. (1) Sunrise for *Anabasis*. (2) Sunrise for *Salsola*. (3) Sunset for *Salsola*. (4) Sunset for *Anabasis*.

graph 2 (p. 345), after the sky had been overcast, there was a calm period of one hour from 13 to 14 o'clock. The evaporation curves fell considerably at this period, whereas the curve of the water-saturation-deficit continued to

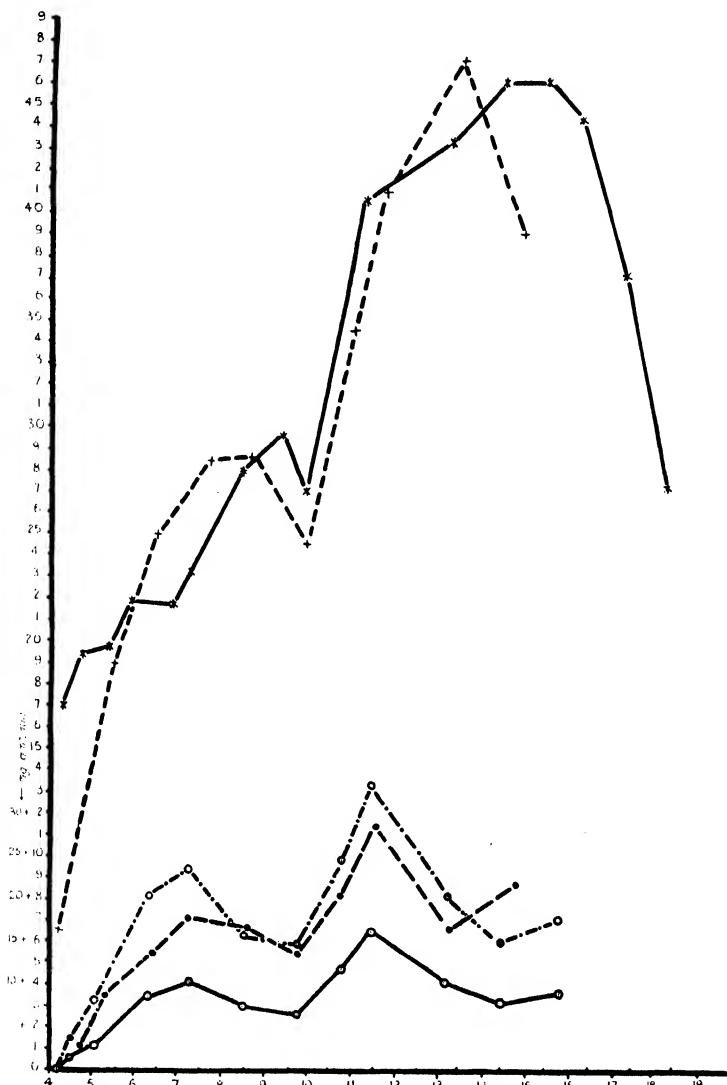
rise. The transpiration of the plants was affected in different ways. *Retama* and *Suaeda* showed a rise in transpiration, whereas the other plants showed a diminution. This reduction in transpiration was much less than that which



GRAPH 11.—Fresh-weight transpiration, surface transpiration, and water-content transpiration on 26. iv. 34. Scale: fresh-weight transpiration, 0–45 mg./g./min.; surface transpiration, 0–50 mg./dm.²/min.; water-content transpiration, 0–45 mg./g./min.; evaporation 0–45 mg./min.; water-saturation deficit in mm.

results from a movement of the stomata. A further example showed a somewhat different effect on 18. vii. 34 at Station 2, graph 12 (p. 357). A short calm

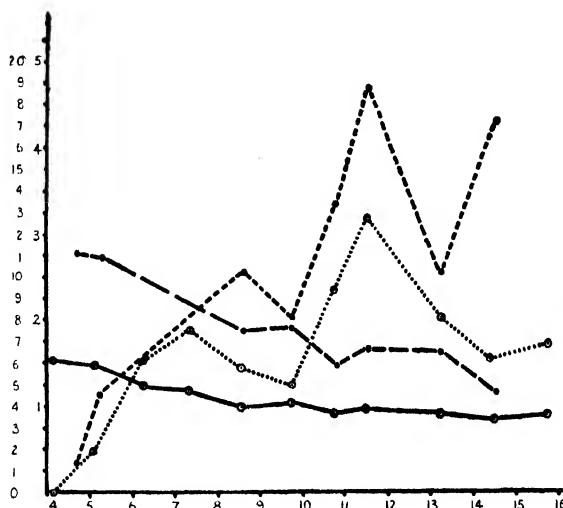
in the morning showed a distinct influence on the evaporation and water-saturation-deficit curves, which fell. The transpiration of *Anabasis* and *Atriplex* decreased.



GRAPH 12.—Fresh-weight transpiration and surface transpiration, evaporation, and water-saturation deficit on 18. vii. 34. Scale: transpiration, 0-94 mg./g./min.; surface transpiration, 0-30 mg./dm.²/min.; evaporation, 0-49 mg./min.; water-saturation deficit in mm. Fresh-weight transpiration of *Anabasis* = \odot — · — \odot . Surface transpiration of *Anabasis* = \odot — · — \odot .

Wind appears to increase the transpiration of the plants. This opinion is in agreement with that of most ecologists and physiologists in recent times (Firbas, 1931 *a*; Stalfelt, 1932; Stocker, 1931, 1933, and 1935; Harder, 1935).

In concluding this section, we may say that, apart from the influence of the water-saturation-deficit, the large fluctuations in the transpiration curves are mainly caused by the movements of the stomata due to the influence of the direct rays of the sun and of the water conditions of the plant. There must also be some effect on the water-saturation-deficit produced by the overcasting of the sky, but the question of how great a part it plays in transpiration is unknown.



GRAPH 12 a.—Water content transpiration and $\frac{\text{water-content}}{\text{dry weight}}$ quotient on 18. vii. 34,

Scale : transpiration, 0-20 mg./g./min. Quotient, 0-5.

Anabasis w/d. quotient ($\odot - \odot$), *Anabasis* water-content transpiration ($\odot \dots \odot$).
Atriplex w/d. quotient ($\cdot - \cdot - \cdot$), *Atriplex* water-content transpiration ($\cdot - \cdot - \cdot$).

(C) *A comparison of transpiration results from the various methods of estimation.*—The curves of water-content transpiration are without exception parallel to those of fresh-weight transpiration, due to the fact that water-content is a decisive factor in fresh weight. The curves of surface transpiration often show no such parallelism (explanation in Stocker, 1931, 1933, and 1935).

The species with which we experimented can be arranged in order, the relationship between the surface and water-content transpiration and the fresh-weight transpiration being taken as unity (Table III, p. 359). When fresh-weight transpiration in relation to surface transpiration (Table III, 2nd column) is considered, the order is as follows :—*Suaeda*, *Reseda*, *Atriplex*.

Heliotropium, *Haplophyllum*, *Erodium*, *Zygophyllum*, *Retama*, *Anabasis*. Here *Suaeda* shows the smallest and *Anabasis* the largest comparative figure. There is a big gap between *Zygophyllum* and *Retama*, so that *Anabasis* and *Retama* constitute a group by themselves. The sequence is altered when the relation of water-content transpiration to fresh-weight transpiration is considered. It is then *Zygophyllum*, *Suaeda*, *Reseda*, *Erodium*, *Haplophyllum*, *Salsola*, *Heliotropium*, *Anabasis*, *Atriplex*, *Retama* (Table III, 3rd column).

(D) *The daily curves of the quotients $\frac{\text{water-content}}{\text{dry weight}}$ and the daily curves of transpiration* (graphs 2 a, 3 d, 7 a, and 12 a).—According to Welton (1933), the hydratur can be measured by substituting the relative water-content or the

TABLE III.—*Average daily totals of transpiration in the three systems of measurement (between 8 and 17 o'clock)*. Milligrams per gram per hour and milligrams per square decimetre per hour. Fresh-weight transpiration is taken as unity.

Plant.	Fresh-weight transpiration. mg./g./h.	Surface transpiration. mg./dm. ² /h.	Water-content transpiration. mg./g./h.
<i>Anabasis</i>	1	6.6	1.7
<i>Retama</i>	1	4.7	2.1
<i>Zygophyllum</i>	1	3.2	1.2
<i>Erodium</i>	1	2.4	1.4
<i>Heliotropium</i>	1	2.0	1.5
<i>Reseda</i>	1	1.8	1.3
<i>Atriplex</i>	1	1.9	1.8
<i>Suaeda</i>	1	1.7	1.3
<i>Haplophyllum</i>	1	2.1	1.4

water-content-deficit instead of the osmotic value. As the dry weight remains practically constant during the course of one day, the quotient $\frac{\text{water-content}}{\text{dry weight}}$ gives a good estimate of the water-content of the organs examined. Its daily course gives the fluctuations of the relative water-content during one day. The plants with a slight daily fluctuation show a low average annual value of water-content (*Retama*, *Anabasis*). The biggest fluctuations are shown by the plants with the highest $\frac{\text{water-content}}{\text{dry weight}}$ values.

It may be said that, very roughly, the higher the water-content, the greater the daily fluctuations in the water-content. Table IV (p. 360) illustrates this, but with *Zygophyllum* as an exception.

The water-content curves of all plants from 14. ii. 34 to 29. ix. 34 (graphs 3 d, 7 a, pp. 348 & 353) become more even and regular and approach a line parallel to the x -axis. On 24. xi. 34 (graph 8 a, p. 354) the curves become more irregular. The reason of this is as follows:—

A comparison of the annual $\frac{\text{water-content}}{\text{dry weight}}$ quotient of any plant with the daily fluctuations (Table V, p. 361) shows that, as the first value falls, the differences between the daily maximal and minimal values of the quotient

TABLE IV.—*The quotient $\frac{\text{water-content}}{\text{dry weight}}$ on 14. ii. 34 and the difference between the smallest and largest daily values.*

Plant.	Water-content Dry weight w./d.	Difference between the smallest and largest daily values.
<i>Retama</i>	1.175	0.24
<i>Heliotropium</i>	2.65	0.67
<i>Salsola</i>	3.8	1.25
<i>Haplophyllum</i>	4.72	1.49
<i>Reseda</i>	5.04	1.55
<i>Erodium</i>	5.47	1.82
<i>Zygophyllum</i>	6.01	0.89
<i>Suaeda</i>	7.63	3.28

become smaller. There are several exceptions to this rule. In the case of *Retama*, where the $\frac{\text{water-content}}{\text{dry weight}}$ values fall very slightly during the summer, the daily differences are small and therefore inexact. *Haplophyllum* shows two exceptions and *Salsola* one.

The relationship between water-content transpiration and $\frac{\text{water-content}}{\text{dry weight}}$ curves is not quite clear. There are a number of cases where the curve is so irregular that no relationship is evident. In some cases, e.g. *Suaeda* and *Zygophyllum* on the date 20. iii. 34 (graphs 3 c and 3 d), the curves run nearly parallel to each other. In the greatest number of cases the curves of water-content and water-content transpiration run counter to each other—

14. ii. 34 (graphs 2 and 2 a). *Haplophyllum*, *Salsola*, *Heliotropium*, and to a lesser extent *Reseda*.

20. iii. 34 (graphs 3 c and 3 d). *Haplophyllum*, *Salsola*, *Reseda*, and *Erodium*.
 30. v. 34. *Haplophyllum*, *Reseda*, *Atriplex*, *Retama*.
 26. vi. 34. *Salsola*, *Atriplex*, *Heliotropium*.
 24. xi. 34 (graphs 8 and 8 a). *Haplophyllum*, *Salsola*, *Heliotropium*, *Erodium*, and *Suaeda*.

This counter-running of the curves denotes the fact that when the water-content is lowest the transpiration is large and vice versa.

The parallelism of the curves denotes that a high water-content is associated with a high transpiration value, and when the water-content is low the transpiration is small.

The parallelism of the curves seems more natural than the counter-action of both curves. The following facts may explain the result. When the water-content of the soil is such that water lost by transpiration cannot be replaced

TABLE V.—*The quotient $\frac{\text{water-content}}{\text{dry weight}}$ and the difference between the largest and smallest daily values.*

Day.	<i>Heliotropium</i> .		<i>Haplophyllum</i> .		<i>Salsola</i> .	
	w./d.	Diff.	w./d.	Diff.	w./d.	Diff.
14. ii. 34	2.65	0.67	4.72	1.49	3.8	1.25
20. iii.	2.33	0.66	4.68	1.40	3.57	0.19
30. v.	1.49	0.42	2.11	0.85	2.51	0.58
26. vi.	1.54	0.70	2.27	0.96	1.98	0.54
4. viii.	2.05	0.72	1.94	0.96	1.41	0.43
29. ix.	1.66	0.22	2.47	2.03	1.36	0.38
24. xi.	2.32	1.25	2.69	1.82

immediately, and when the water-condition of the plant is on the whole sub-optimal, the water-content depends mainly on the amount of transpiration.

If the transpiration rises, the water-content and the quotient $\frac{\text{water-content}}{\text{dry weight}}$

will fall. If transpiration falls the water-content will rise ; the water recovered will not be given out immediately, but can be stored. The falling and rising of transpiration represents a compromise between the effort to prevent the water-content falling below a certain value or measure and the necessity of transpiring and of leaving the stomata open for the exchange of gases. We cannot tell how far an 'incipient drying' in addition to the movement of the stomata is concerned in the production of the counter-running curves. The self-regulating mechanisms described do not prevent the falling of the water-content in the hot summer months.

We can only hint at an explanation of the parallelism of the curves which sometimes occurs (graphs 3 c and 3 d, p. 348). As the transpiration rises the water-reserve rises, the water sucked up is not entirely given out, but is in part stored up. When a water-content higher than the optimum is reached, a passive closing of the stomata ensues (Stalfelt, 1932). Transpiration then falls and also the water-content. When the water-reserve has sunk to a certain point, a passive opening of the stomata follows. This hypothesis is supported by the fact that parallelism of the curves occurs only in the case of succulents with a big water-reserve, as was the case on 20. iii. 34, and it is never observed in the dry season.

(2) *The annual course of the curves.*

In order to get an accurate idea of the annual water-balance of the plants it is necessary to find the amount of water transpired annually per gramme of fresh weight. This is essential, as a number of the plants transpire continually during the summer, whereas in others transpiration ceases during that period owing to the absence of transpiring organs (Table VI, opposite). The total values on the various days were regarded as typical for the respective months. The total value for each month was calculated. The values for the month in which no measurements were made were estimated from those of the preceding and following months. The results show exactly the same sequence with regard to the *fresh-weight transpiration* and *water-content transpiration* and *relative average amount of transpiration*. The sequence is altered when *surface transpiration* is considered. Compare Tables VI and X (pp. 363 and 368). It is necessary also for the complete investigation of the water balance to find the annual amount of water transpired by each plant. Plants of average size and development were chosen for those calculations (Table XI, p. 370). It is interesting to compare these figures with the results of Stocker (1935).

(a) *Transpiration. Fresh-weight transpiration.*—From the results (Table VI, opposite) the plants may be divided into two groups according to their *fresh-weight transpiration* :—

(1) Plants with low transpiration : these arranged in order of increasing transpiration are :—*Suaeda*, *Zygophyllum*, *Atriplex*, *Salsola*, *Retama*. This series varies slightly on different days. Including Station 2, *Anabasis* is seen to belong to this group.

(2) Plants with high transpiration :—*Erodium*, *Reseda*, *Heliotropium*, *Haplophyllum*. In this series there are more variations than in the first group. On one day (30–31. v. 34) the limits between the two groups are indistinguishable (graph 4).

Surface transpiration.—As regards the surface transpiration the grouping varies as follows :—*Retama* and *Anabasis* change over to the high-transpiration group.

Water-content transpiration.—As regards the *water-content transpiration* the low-transpiration group again consists of *Suaeda*, *Zygophyllum*, *Atriplex*,

TABLE VI.—*Daily totals of transpiration in the three systems of measurement from sunrise to sunset.*

On each day column 1 gives fresh-weight transpiration (F.W.T.).

column 2 gives surface transpiration (S.T.).

column 3 gives water-content transpiration (W.C.T.).

Date . . .	14. ii. 34.	20. iii. 34.	30/31. v. 34.	26/27. vi. 34.	4. viii. 34.	29. ix. 34.	24. xi. 34.
Plant:	F.W.T. mg./dm. ²	S.T. mg./g.	W.C.T. mg./dm. ²	F.W.T. mg./g.	S.T. mg./g.	W.C.T. mg./dm. ²	F.W.T. mg./g.
<i>Retama</i> . .	4273 20568	8352	5350 30708	9734 4887 22916	10077 3381 16629	8511 3081 13565	7022 2170 8991
<i>Salsola</i> . .	2835 . .	3628	4245 ..	5451 2400 ..	3357 2706 ..	4007 1887 ..	3243 1600 ..
<i>Haplo-</i> <i>phyllum</i> }	18503 51000	21094 26942	83407 32369	6833 11027 10027	13668 24716 28907	13641 20760 20819	11319 20365 16076
<i>Reseda</i> . .	11490 24518	13517 21906	47531 28453	6705 9577 8693
<i>Helio-</i> <i>tropium</i> }	14352 21858	19023 8914	15609 12327	7578 14272 11911	9714 21783 16278	15231 40792 22428	5574 11720 8624
<i>Atriplex</i>	1107 1923 1726	2406 4254 4383	1149 2055 2292	2349 5613 4044 ..
<i>Erodium</i> *	10903 26514	12957 9125	23291 11097	6696 18626	8624
<i>Zygo-</i> <i>phyllum</i> }	1817 7291	2121 1185	3652 1417	1839 5069	2389
<i>Suaeda</i> . .	1158 2950	1321 2900	4676 3562
Date . . .	9. viii. 33. 20. xi. 33.	26. iv. 34.	18. vii. 34.				
Plant:	mg./g.	mg./g.	mg./dm. ²	mg./dm. ²	mg./g.	mg./dm. ²	mg./g.
<i>Anabasis</i> .	1019	1112	2727	22095	3918	2589	13671 5124

Salsola, *Anabasis*. The high-transpiration group consists of *Erodium*, *Reseda*, *Heliotropium*, *Haplophyllum*. *Retama* takes a middle position, with the following exceptions :—

On 30. v. 34 it occupied a position in the middle of group 2. Towards the end of the year when its water-reserve is exhausted it is included in group 1, as is the case when *fresh-weight transpiration* is considered. In Table VII (p. 365) the transpiration values of the plants between 8 and 17 o'clock are given. The transpiration values of *Retama* are taken as unity.

In Table VIII (p. 365) the daily amount of surface transpiration of each plant is shown in relation to that of 14. ii. 34, which is taken as unity. (In the case of *Salsola* the *fresh-weight transpiration* is introduced, since the *surface transpiration* could not be accurately estimated.)

The plants may be divided into three types on whichever system we base our conclusions :—

(1) Plants in which the transpiration rises steadily from 14 February to 20 March and falls steadily from that date,—*Retama*.

(2) Plants in which the transpiration rises from 14 February to 20 March (in some it begins to fall on 2 February) and falls steadily until 29 September, after which it begins to rise. In those plants which have no transpiring organs during the summer months transpiration on the 24. xi. 34 is larger than the last measured value,—*Salsola*, *Suaeda*, *Erodium*, and *Reseda*.

(3) Plants in which transpiration falls on 14 February or plants which show a rise in transpiration from 14 February to 20 March followed by a fall. During the rainless summer months there are sudden rises in transpiration on certain days,—*Heliotropium*, *Haplophyllum*, and *Atriplex*.

There is a relationship or more accurately a parallelism between the grades of transpiration and the water-content.

The curves of the annual fluctuations of the $\frac{\text{water-content}}{\text{dry weight}}$ quotients (graph 13, p. 366) show that the values for all plants in groups 1 and 2, with the exception of *Reseda*, fall constantly until 29 September.

From the date 29. xi. 34 to the 24. xi. 34 the $\frac{\text{water-content}}{\text{dry weight}}$ value rises to a figure higher than the final value attained before the disappearance of the vegetative organs. Thus the transpiration value of all plants of group 2 rises, it becomes larger than the previous value. *Suaeda* (24. xi. 34) is a good example of this. The plants of group 3 also show parallelism between the curves of transpiration and $\frac{\text{water-content}}{\text{dry weight}}$ with the exception of *Haplophyllum* (29. ix. 34) and *Atriplex* on 26. vi. 34. The sudden rises of transpiration and $\frac{\text{water content}}{\text{dry weight}}$ value in this group during the dry period (e.g. *Heliotropium* from 30. v. 34 to 26. vi. 34 to 4. viii. 34) are due to the fact that these plants are

TABLE VII.—*Average annual totals of daily transpiration (8–17 o'clock)—milligrams per gram, and milligrams per square decimetre. The value of Retama is taken as unity.*

Plant.	Fresh-weight transpiration.	Surface transpiration.	Water-content transpiration.
	mg./g.	mg./dm. ² .	mg./g.
<i>Retama</i>	1	1	1
<i>Suaeda</i>	0·83	0·22	0·49
<i>Zygophyllum</i>	0·42	0·28	0·26
<i>Salsola</i>	0·95	..	0·64
<i>Erodium</i>	2·96	1·35	1·7
<i>Reseda</i>	3·22	1·15	2·01
<i>Haplophyllum</i>	4·00	1·87	2·63
<i>Heliotropium</i>	3·70	1·67	2·54
<i>Atriplex</i>	0·69	0·33	0·53
<i>Anabasis</i>	0·82	1·15	0·67

TABLE VIII.—*Daily totals of surface transpiration, 8–17 o'clock, referred to the value on 14. ii. 34, which is taken as unity.*

Numbers in brackets give the absolute value on 14. ii. 34.

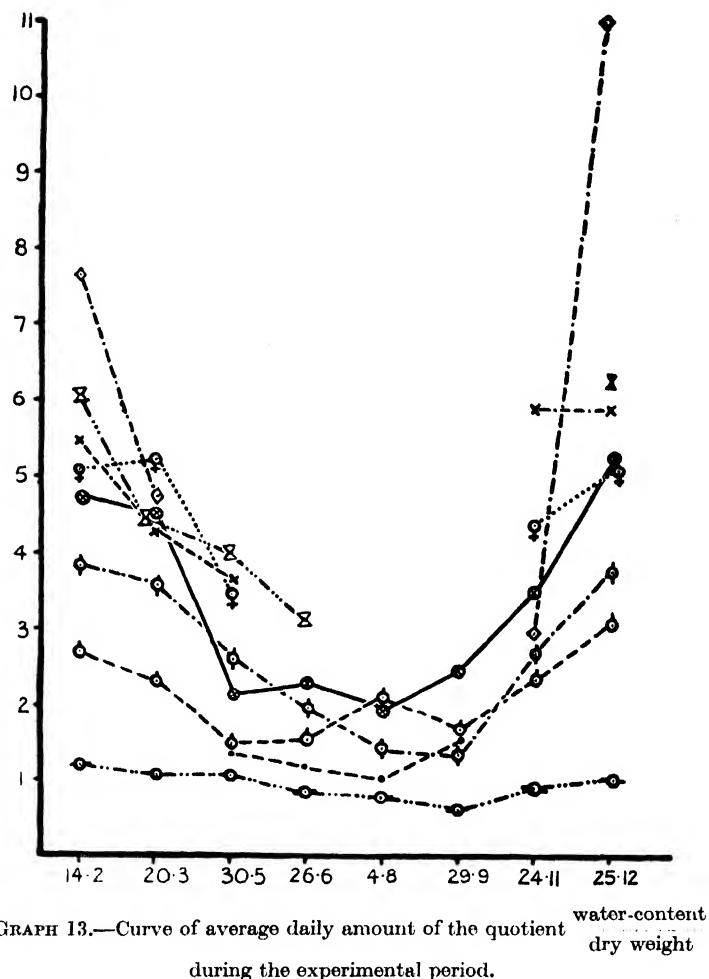
In the case of *Atriplex* the value on 26. iv. 34=1.

„ „ *Salsola* the fresh-weight transpiration was taken as the basis.

Plant.	14. ii.	20. iii.	30/31. v.	26/27. vi.	4. viii.	29. ix.	24. xi.
<i>Retama</i>	1 (14918)	1·47	1·1	0·81	0·66	0·5	0·48
<i>Suaeda</i>	1 (2793)	1·58	0·65
<i>Salsola</i>	1 (2835)	1·5	0·85	0·83	0·54	0·5	0·80
<i>Reseda</i>	1 (15624)	1·91	0·58	0·97
<i>Erodium</i>	1 (16817)	0·88	0·71	1·22
<i>Heliotropium</i> ..	1 (15626)	0·71	0·65	1·22	2·2	0·66	1·39
<i>Haplophyllum</i> ..	1 (25346)	1·49	0·20	0·75	0·71	0·68	1·01
<i>Zygophyllum</i>	1 (6366)	0·47	0·69
<i>Atriplex</i>	0·31	0·63	0·32	0·82	..

decreasing the transpiration surface progressively during the dry season by losing gradually the older leaves. In the younger leaves the water-content is higher, and transpiration values are higher too.

There is a distinct proportion between the height of the daily quotient



GRAPH 13.—Curve of average daily amount of the quotient $\frac{\text{water-content}}{\text{dry weight}}$ during the experimental period.

$\frac{\text{water-content}}{\text{dry weight}}$ and the height of the daily transpiration value, although it is difficult to establish any definite relationship between the hourly readings on any one day.

The $\frac{\text{water-content}}{\text{dry weight}}$ and the annual transpiration curves run counter to those

of soil suction-pressure. We cannot conclude from this that the transpiration is limited by the poor water conditions of the soil in which the plants live, as we cannot calculate the part played by the atmospheric evaporation. To exclude this factor we calculated the *relative transpiration*, although well aware of the arguments against this value (Seyboldt, 1929; Welten, 1933; etc.). We have often observed that atmospheric evaporation-results depend upon the type of evaporimeter used. The use of the *relative transpiration* value does, however, enable us to establish the order of the limits within which the figures vary *. From Table IX (p. 368) the values of *relative transpiration* take, on the whole, the same yearly course as the values of absolute transpiration. We are therefore justified in speaking of the limitation of transpiration, as both the relative and the absolute transpiration show a distinct fall. In Table IX the highest value of *relative transpiration* is taken as 100 and the smaller values calculated as percentages. The results show that the larger the amount of absolute transpiration on days with a good water supply, the larger is the limitation on days with a bad water supply—in other words, the greater the power of transpiration the greater is the power of limiting the transpiration. The results have not been obtained automatically, but with due regard to the condition of the plant. It would not be possible to compare values obtained from old big leaves of *Atriplex* with young small ones. *Suaeda* is found to show the smallest limitation of transpiration and *Haplophyllum* the largest. Plants observed show the following sequence: *Suaeda*—*Atriplex*—*Zygophyllum*—*Retama*—*Heliotropium*—*Reseda*—*Erodium*—*Haplophyllum*. We cannot include *Salsola*, as the figures refer to *fresh-weight transpiration*. This sequence is similar to that obtained when the daily amount of absolute transpiration is considered.

In comparison with the transpiration of plants of other deserts and climates (graph 14, see too Stocker, 1935), the extreme values of all desert habitats stand out. The extremest value is reached by *Haplophyllum*. The plants of Kara-Kum are exceptional for ground water is touched by their roots. But the variety of types of transpiration in one and the same habitat, specially in deserts, is much bigger than the variety of medium values in various habitats (Stocker, 1931, 1933, 1935).

(b) *The various quotients.*—(1) $\frac{\text{Water-content}}{\text{Dry weight}}$. The average annual value of the quotient $\frac{\text{water-content}}{\text{dry-weight}}$ is the best expression of the water reserves of the plant. It may be described as a 'xeromorphic' quotient, since it shows the extent of xeromorphism, a small value of the quotient denoting a high degree of xeromorphism. This is shown by comparing the values of

* Stocker (1935) has also recently pointed out that the determination of *relative transpiration* is indispensable for ecological field experiments.

TABLE IX.—*Relative transpiration.* Surface transpiration was taken as the basis. In the case of *Salsola* fresh-weight transpiration was taken as the basis of calculation. The number in brackets gives the smallest relative transpiration in the percentage of the biggest.

Plant.	14. ii.	20. iii.	30/31. v.	26/27. vi.	4. viii.	29. ix.	24. xi.
<i>Retama</i>	2940	3530	1915	1381	1305	1031 (35.1%)	2160
<i>Salsola</i>	406	489	200	225	182 (28.4 %)	184	640
<i>Haplophyllum</i> ..	7300	9600	917 (9.5 %)	2060	2000	2340	7578
<i>Reseda</i>	3500	5460	798 (14.5 %)	5001
<i>Heliotropium</i> ..	3130	1800	1190	1815 (19.3 %)	3930	1345	6157
<i>Atriplex</i>	160	354	198 (55 %)	645	..
<i>Erodium</i>	3780	2680	1550 (14.4 %)	8001
<i>Zygophyllum</i> ..	1041	412 (39.6 %)	423
<i>Suaeda</i>	422 (83%)	538	480

TABLE X.—*Annual totals of transpiration and annual totals referred to Retama as unity.*

1st column =fresh-weight transpiration.

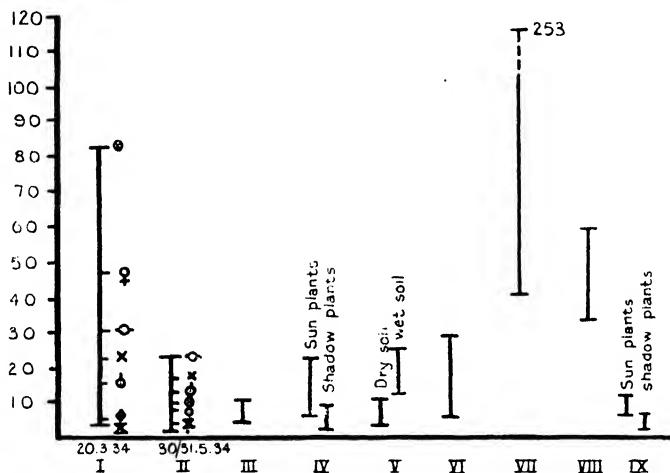
2nd column= surface transpiration.

3rd column =water-content transpiration.

Plant.	Annual total of transpiration in grammes.			Annual total of transpiration— correlated to <i>Retama</i> as unity.		
	g./fr.w.	dm. ² /s.	g./w.c.	g./fr.w.	dm. ² /s.	g./w.c.
<i>Zygophyllum</i>	289	1017	351	0.22	0.16	0.13
<i>Suaeda</i>	315	479	390	0.24	0.08	0.45
<i>Salsola</i>	925	..	1324	0.71	..	0.50
<i>Retama</i>	1309	6381	2654	1	1	1
<i>Erodium</i>	2226	5330	2660	1.69	0.84	1.01
<i>Reseda</i>	2640	5196	3247	2.02	0.81	1.23
<i>Heliotropium</i> ..	3780	7909	5538	2.89	1.24	2.09
<i>Haplophyllum</i> ...	5279	12031	6976	4.02	1.88	2.63

water-content (Table XII, p. 370) with the anatomical classification of species dry weight to be given in a supplementary paper.

It is evident that, though all succulents have a high $\frac{\text{water-content}}{\text{dry weight}}$ value, yet all plants with this high value are not succulents. For example, *Erodium* has a higher $\frac{\text{water-content}}{\text{dry weight}}$ value than the succulent *Zygophyllum*.



GRAPH 14.—Daily amount of surface transpiration. Plants of the Judaean desert compared with other deserts. Scale, 0–120 mg./dm.².

I & II. Desert of Judaea. III. Lapland (Stocker, 1931). IV. Tyrol (Piscek & Cartellieri, 1933). V. Hungary (Stocker, 1933). VI. Arizona (Schratz, 1931 c). VII. Kara-Kum (Wassiljiew, 1931). VIII. Algeria (Harder, 1933). IX. Java (Stocker, 1935).

(2) $\frac{\text{Water-content}}{\text{Surface}}$. The annual curve of the quotient $\frac{\text{water-content}}{\text{surface}}$ is in most cases parallel to the annual curve of the quotient $\frac{\text{water-content}}{\text{dry weight}}$ (Table XII, p. 370). The table also shows that the quotient $\frac{\text{water-content}}{\text{surface}}$, as Stocker has pointed out, cannot be regarded as a measure of succulence. (See *Retama*, Table XII.)

The two quotients $\frac{\text{water-content}}{\text{dry weight}}$ and $\frac{\text{water-content}}{\text{surface}}$ together give an admirable means of measuring succulence, as high values of both quotients characterize this group.

(3) Surface Fresh weight . The average annual value of this quotient is the only value worth consideration. Succulents and full xeromorphics, both of which have small surfaces, show the lowest values of the quotient, while the group *Heliotropium-Atriplex* shows the highest values.

TABLE XI.—*Annual amount of water consumption per individual plant in kilogrammes.*

Plant.	Kg. water.
<i>Retama</i>	1500–3500
<i>Suaeda</i>	300–400
<i>Salsola</i>	50–100
<i>Zygophyllum</i>	30–120
<i>Haplophyllum</i>	20–40
<i>Heliotropium</i>	20–30
<i>Erodium</i>	20–25
<i>Reseda</i>	15–20

TABLE XII.—*Annual average values of the dimension quotients.*

$$a = \frac{\text{water-content}}{\text{dry weight}}, b = \frac{\text{water-content}}{\text{surface}}, c = \frac{\text{surface}}{\text{fresh weight}}, d = \frac{\text{surface}}{\text{dry weight}}, e = \text{water-content in percentage of fresh weight}.$$

Plant.	a.	b.	c.	d.	e.
	w./d.	w./s.	s./f.w.	s./d.	w.c. in % of f.w.
<i>Retama</i>	0.92	2.3	0.254	0.42	58.5 %
<i>Atriplex</i>	1.62	1.08	0.53	1.18	57 %
<i>Anabasis</i>	1.68	5.25	0.135	0.30	69 %
<i>Heliotropium</i>	2.13	1.35	0.472	1.61	64 %
<i>Salsola</i>	2.63
<i>Haplophyllum</i> ...	3.35	2.11	0.377	1.91	79 %
<i>Reseda</i>	4.61	1.63	0.510	3.07	82 %
<i>Zygophyllum</i>	4.74	3.47	0.248	..	86 %
<i>Erodium</i>	5.04	2.01	0.430	3.09	86.5 %
<i>Suaeda</i>	5.87	3.04	0.301	3.59	91 %

(4) $\frac{\text{Surface}}{\text{Dry weight}}$. This quotient behaves exactly as the quotient $\frac{\text{water-content}}{\text{dry weight}}$, and is an equally good indication of xeromorphism and the presence of xeromorphic characteristics.

(5) Water-content. This, expressed as a percentage of fresh weight, is shown in the last column of Table XII.

Summing up, we may say that :

(a) full succulents are characterized by high values of $\frac{\text{water-content}}{\text{dry weight}}$,
 $\frac{\text{water-content}}{\text{surface}}$, and $\frac{\text{surface}}{\text{dry weight}}$, and a low value of $\frac{\text{surface}}{\text{fresh weight}}$;

TABLE XIII.—*Water-saturation deficit of plants.*

Daily water-saturation deficit in percentage of the highest water-content on the same day.

The top bracketed numbers are the latent water-saturation deficit.

The lower bracketed numbers are the maximum water-saturation deficit of the same plant during the course of the year, in percentage of the maximum water-content.

Date	14. ii.	20. iii.	30. v.	26. vi.	4. viii.	29. ix.	24. xi.
Plant :							
<i>Retama</i>	19 (0)	11 (12)	19 (12)	13 (31)	16 (31)	16 (37) (47)	13 (28)
<i>Suaeda</i>	36 (16)	24 (46) (64)	44 (61)
<i>Salsola</i>	29 (0)	5 (21)	38 (26)	32 (50)	24 (66) (74)	27 (65)	52 (25)
<i>Reseda</i>	18 (5)	11 (0)	29 (31) (52)	7 (24)
<i>Erodium</i>	30 (11)	31 (22)	40 (33) (59)	38 (0)
<i>Heliotropium</i>	23 (5)	24 (12)	25 (44)	36 (32) (54)	29 (21)	13 (43)	45 (9)
<i>Haplophyllum</i>	26 (0)	26 (6)	31 (53)	34 (51)	40 (59) (75)	39 (45)	8 (39)
<i>Zygophyllum</i>	14 (0)	23 (22)	15 (35) (45)
<i>Atriplex</i>	17 (58)	33 (61)	33 (67) (78)	40 (45)	..

(b) full xeromorphics are characterized by low values of $\frac{\text{water-content}}{\text{dry weight}}$,
 $\frac{\text{surface}}{\text{fresh weight}}$, and $\frac{\text{surface}}{\text{dry weight}}$, and high values of $\frac{\text{water-content}}{\text{surface}}$;

(c) the other herbaceous plants fall between these two extremes, according to whether the succulent or xeromorphic characteristics predominate. The quotients also afford valuable indications of the habitat conditions.

(c) *Water-saturation deficit*.—Here we are concerned with two values, the daily water-saturation deficit in which the lowest water-content in the course of one day is expressed as a percentage of the highest, and the latent water-saturation deficit which the plant possesses in the morning before transpiration begins (morning-water-content-deficit of Welten). To obtain this latter quantity the maximum daily water-content value is expressed as a percentage of the maximum annual water-content value. (See Table XIII, p. 371, which also shows the maximum water-saturation deficit.) Table XIII shows the following facts :—Firstly, there is no relationship between the extent of daily water-saturation deficit and the quotient $\frac{\text{water-content}}{\text{dry weight}}$; secondly, the annual curves of the latent water-saturation deficit and of the $\frac{\text{water-content}}{\text{dry weight}}$ quotient run counter to each other, i.e. in the rainless season the water-saturation deficit increases from month to month, with the exceptions of *Heliotropium* and *Haplophyllum* (for explanation, see p. 376). We can therefore arrive at the conclusion that desert plants are characterized by the power of withstanding without injury a large water-saturation deficit which would prove lethal for other plants.

Comparing our figures of the daily water-saturation deficit with those of Wassiljew (1931), Livingston and Brown, Krassnoselsky-Maximov, and Iljin, we see that our results particularly in the case of *Salsola* (52 per cent.) show a greater average value, comparable only with the value of plants of the Arizona desert.

The supplementary paper, already referred to, is in two parts, entitled 'Root conditions of certain plants of the Judaean desert' and 'The physiological anatomy of the transpiring organs and the conduit system of certain typical plants of the Judaean desert'.

(3) *The water balance of the plants observed.*

(1) *Retama*. The water balance of *Retama* is extremely constant, and of all the plants observed *Retama* uses the largest quantity of water. This amounts to 1500–3500 kg. per annum. It has the deepest and most extensive root-system. We calculate that a plant which uses 1500 kg. of water per annum has a rooting system which covers an area of 38 to 39 sq. metres. The rainfall over this surface would be on average 3900 kg.—that is, $2\frac{1}{2}$ times as much as the plant requires.

Retama only grows where the soil has a low salt-content. It is specially well adapted to make the best possible use of the existing ground water. If we assume that $1\frac{1}{2}$ times the amount of water taken up cannot be given out, we have a water

TABLE XIV.—Station 1.

Date.	Cloud and wind.	Atmospheric temperature.	Soil-water and suction-pressure.	Rain for the season.	Transpiration curves.	Vegetation.
3. i. 34.	mm. 7.0	Graph 1.	No annuals. <i>Zygophyllum</i> without new shoots. <i>Erodium</i> and <i>Heliotropium</i> a few leaves. <i>Suaeda</i> , <i>Reseda</i> , <i>Hippophae</i> just sprouting.
14. ii. 34.	Midday sun over east. Period of calm; then steadily changeable wind.	Low. Max. at 14.40 p.m. 20° C.	Table I a.	81.5	Graph 2. w./d. curve. Graph 2 a.	Slopes covered with green seedlings. All perennials sprouting. <i>Reseda</i> , <i>Zygophyllum</i> , <i>Heliotropium</i> , flower-buds present.
20. iii. 34.	No cloud. Slight steady breeze.	Max. at 14.0 p.m. 28°.7 C.	Table I b.	85.5	Graph 3. Graph 3 a. Graph 3 b. Graph 3 c. w./d. curve. Graph 3 d.	Annuals flowering. <i>Suaeda</i> beginning to flower. <i>Retama</i> , <i>Zygophyllum</i> fruiting. All plants wilt at midday.
30/31. v. 34.	No cloud. Practically no wind.	Max. 33° 0 C.	Table I c.	94.5	Graph 4. Graph 4 a.	No annuals. <i>Suaeda</i> fruiting. <i>Retama</i> ripe seeds and new shoots woody. <i>Heliotropium</i> , <i>Heliotropium</i> flowering, <i>Reseda</i> over. <i>Erodium</i> and <i>Zygophyllum</i> fruiting.
26/27. vi. 34.	No cloud. Wind changeable, warm, westly after sunset. Chamssine and Fœhn.	Maxima 13.0 p.m., 36°.0 C. 15.30 p.m., 36°.5 C.	Table I d.	Graph 5.	<i>Erodium</i> and <i>Reseda</i> disappeared. <i>Zygophyllum</i> no leaves remain. <i>Heliotropium</i> and <i>Hippophae</i> ripe seeds (only young small leaves left). <i>Atriplex</i> , <i>Retama</i> no change. <i>Salsola</i> beginning to flower.
4. vii. 34.	No cloud ; slight wind.	Max. 38° C.	Table I e.	Graph 6.	<i>Salsola</i> fruiting. <i>Atriplex</i> , <i>Heliotropium</i> drying. <i>Retama</i> no change.
29. ix. 34.	No cloud ; slight wind.	22°.0 at sunrise. Max. 33°.5 C. at 13 p.m.	At 50-60 cm. depth, < 4 mol. NaCl.	Graph 7. w./d. curve. Graph 7 a.	Little change.
24. xi. 34.	Cloud variable.	Max. at 11.40 a.m. 24° C.	Table I f.	4.5	Graph 8. w./d. curve. Graph 8 a.	<i>Suaeda</i> and <i>Erodium</i> new shoots and leaves.

TABLE XV.—Station 2.

Date.	Cloud and wind.	Atmospheric temperature.	Soil-water and suction-pressure.	Rain for the season.	Transpiration curves.	Vegetation.
9/10. viii. 33.	No cloud. Almost windless.	Max. 36°·5 C. Min. 22°·0 C.	Summer drought.	Graph 9.	<i>Anabasis</i> , <i>Salsola</i> , <i>Atriplex</i> the only active plants.
20. xi. 33.	No cloud. East wind in the morning. Warm west wind between 14 and 15 p.m.	Max. at 11 a.m. 25°·0 C., at 14 p.m. 25°·0 C.	Nine days before rainy season.	Graph 10.	<i>Anabasis</i> and <i>Salsola</i> fruiting. <i>Atriplex</i> almost leafless.
18. i. 34.	Max. 18°·8 C.	Table I g.	59·0 mm.	<i>Anabasis</i> withered. <i>Salsola</i> new shoots. <i>Atriplex</i> new leaves. Bulbous plants with rosettes of leaves. <i>Bellardia desertorum</i> especially noticeable. Many seedlings, mosses, liverworts, protonemata, and lichens.
26. iv. 34.	No cloud. Hot east wind (chamssine). Later in the day west wind and dust-storm.	Max. 37°·5 C.	At 50 cm. depth. Water-content 4·65 %.	92·5 mm. since rainy season began.	Graph 11.	<i>Anabasis</i> new shoots. Some annuals flowering. Other annuals finished flowering.
18. vii. 34.	Almost cloudless. Calm in the morning. Between 14.10 p.m. and 16 p.m. storm and hurricane.	Max. in the sand-storm 44°·0 C.	Suction-pressure 4 mol. NaCl. At 40 cm. depth. Suction-pressure 3·2 mol. NaCl.	Graph 12. w/d. curve. Graph 12 a.	Annuals and geophytes disappeared. <i>Salsola</i> , <i>Atriplex</i> , and <i>Anabasis</i> active. <i>Salsola</i> in flower.

balance in which the intake and output are in equal proportion. The daily *fresh-weight transpiration* and *water-content transpiration* are very small and the *surface transpiration* is very big.

The annual amount of *fresh-weight transpiration* and *water-content transpiration* is smaller than those values for the herbaceous plants which do not survive the summer in an active state, but the annual amount of *surface transpiration* is larger than the same values for these plants. It is smaller than the values for *Heliotropium* and for *Haplophyllum*. The transpiration limitation in the summer months amounts to 35 per cent., i.e. it is not very large in comparison with the extent of limitation of other plants which transpire during the summer.

The daily *water-saturation deficit* is about the same each day, and shows the lowest average value 15 per cent. The *latent water-saturation deficit* rises slowly in the summer months to the value of 37 per cent., the lowest value shown by plants that transpire during the summer.

The daily and annual fluctuations in the water-content and the daily fluctuation in the amount of transpiration are very slight.

On the whole, the water balance is very stable.

(2) *Suaeda*.—The plant loses its transpiration organs early in the year and remains almost dormant during the 6 or 7 summer months. In spite of this fact, with the exception of *Retama*, *Suaeda* uses the most water per annum, probably because of the large number of leaves on each plant. About 300 to 400 kg. of water is transpired annually. The rooting system covers an area of 10 to 12 square metres, affording 1060–1272 kg. of water—about three times that required.

Suaeda differs from *Retama* in that its roots lie in the top 5 cm. of soil, which layer dries soon after the cessation of rain. *Suaeda* belongs to the 'drought evaders'. Due to the lethargy of the stomatal apparatus, limitation of transpiration is incomplete, amounting only to 17 per cent. The fluctuations of both daily and annual water-content are larger than those of any other plant examined. The average daily saturation deficit of 35 per cent. is very large (cf. *Erodium*). The latent water-saturation deficit is high, and exceeds that of *Retama* and *Haplophyllum*. Daily fluctuations of transpiration are small.

(3) *Zygophyllum*.—The water balance is more economical than that of *Suaeda*, as shown by the small value of the daily average water-saturation deficit (17 per cent.), the fluctuations of the water-content, and the amount of transpiration. Of all the plants examined, *Zygophyllum* shows the smallest annual value of *fresh-weight transpiration* and *water-content transpiration*. For this reason the dormant season is shorter than that of *Suaeda*.

Owing to the irregular formation of the root system, it is difficult to calculate the amount of water used.

(4) *Haplophyllum*.—About 20–30 kg. of water is transpired annually, whereas the available water supply in the soil covered by the roots is 200 kg., about 5–10 times the required amount. Almost the same may be said for *Heliotropium*, *Erodium*, and *Reseda*.

Amongst the plants measured, this plant shows the greatest value for the daily and annual amounts of transpiration in all systems of measurement. It also shows the greatest transpiration limitation (90·5 per cent.).

The average daily latent water-saturation deficit and the maximum water-saturation deficit are large. The annual water-content fluctuation is the largest of those measured, the daily fluctuations in amount of transpiration are also large, but the daily fluctuations of water-content are smaller than those of *Erodium* and *Reseda*.

The plant is able to survive the dry season in an active state, owing to the fact that it limits the transpiring surface and the transpiration. It has also the power of withstanding a high water-saturation deficit.

(5) *Heliotropium*.—The water balance is more constant than that of *Haplophyllum*, as is shown by the water-saturation deficit and the water-content. The transpiration limitation is large, 80·7 per cent. The stomatal apparatus reacts promptly to exterior and interior conditions. The amount of daily and annual transpiration in all three systems of measurement is very large, as is also the average daily water-saturation deficit.

The daily fluctuations in water-content are small, and the annual fluctuations in water-content are the lowest among the herbaceous plants.

The progressive limitation of the transpiring surface during the dry period is much larger than that of *Haplophyllum*.

(6 and 7) *Erodium* and *Reseda*.—Transpiration in all systems of measurement is large, as are also the daily fluctuations. The annual and daily fluctuations in water-content are also large. The latent water-saturation deficit is small. The total amount of water used annually is nearly as great as that required by *Heliotropium* and *Haplophyllum*, owing to the fact that the leaves of *Erodium* and *Reseda* are numerous and large.

(8) *Atriplex*.—Of all the plants which survive the summer in an active state, *Atriplex* shows the smallest value of transpiration limitation (45 per cent.). Transpiration and daily fluctuations of transpiration in all systems of measurement are small.

The latent daily and maximal water-saturation deficit are large, the latter reaching 78 per cent., which is the largest value found in any of the plants examined.

Summarizing the results of an examination of the water balance of the plants examined, we find that they survive the summer dry season in the following ways :—

(1) They discard the transpiration organs and so remain dormant—e.g. *Suaeda*, *Zygophyllum*, *Erodium*, and *Reseda*.

(2) They increasingly reduce their transpiring surface—e.g. *Heliotropium*, *Haplophyllum*, and *Atriplex*.

(3) They have the power of withstanding a large water-saturation deficit—e.g. *Haplophyllum* and *Atriplex*.

(4) They have the power of limiting transpiration—e.g. *Haplophyllum* and *Heliotropium*.

(5) They have an even water balance which shows no large fluctuations of water-saturation deficit and water-content—e.g. *Retama* and *Anabasis*.

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SUMMARY.

Ecological observations were made on certain plants of the Judaean desert. A special study was made of the transpiration conditions. Using Huber's method of weighing cut branches, the transpiration of the plants was calculated. Fresh-weight transpiration, surface transpiration, water-content transpiration, and relative transpiration results were obtained.

The quotients $\frac{\text{water-content}}{\text{dry weight}}$, $\frac{\text{water-content}}{\text{surface}}$, and water-saturation deficit of the plants were also calculated. These quotients are useful in that they throw light on conditions of transpiration and assist in the grouping of species. They afford valuable indications of habitat conditions. These two quotients together give an admirable means of recognizing succulence. A high $\frac{\text{water-content}}{\text{dry weight}}$ and high $\frac{\text{water-content}}{\text{surface}}$ are the best indications of this group.

The difference between full xeromorphics and herbaceous plants with xeromorphic characters comes out clearly. All succulents have high $\frac{\text{water-content}}{\text{dry weight}}$ value, but all plants with high $\frac{\text{water-content}}{\text{dry weight}}$ are not succulents. The smaller the water-content the smaller the quotient and the more pronounced are the xeromorphic characters.

The plants studied were of different types, and were found to show different methods of withstanding the conditions of life in their habitat:—

1. Succulents, e.g. *Suaeda* and *Zygophyllum*.

These plants gradually lose their leaves in the beginning of the drought period, and so are not physiologically active in summer. They show a low transpiration in all systems of measurement, the water balance is uneven, and the transpiration limitation incomplete. *Suaeda* is one of the first perennials to dry up. These plants are an example of the fact that a low transpiration does not bring about an even water balance and capacity for drought resistance. They are dependent on external conditions.

2. *Xeromorphic leafless plants, e.g. Anabasis and Retama.*

These plants are in a physiologically active state throughout the year. Transpiration in relation to fresh and dry weight is small, but in relation to surface is great (although not as great as the strongly transpiring xerophytes). The water balance is even and the transpiration limitation is small. These plants are much more independent of external factors than the other xerophytes.

3. *Herbaceous xerophytes, e.g. Erodium, Reseda, Heliotropium, and Haplophyllum.*

All these are characterized by high transpiration values in all systems of measurement and by great power of limitation of transpiration by stomatal movement. They may be divided into two groups :—

(a) Those without xeromorphic characters which do not survive the dry season in an active state, e.g. *Erodium* and *Reseda*.

(b) Those which lose their leaves gradually and so are active, though decreasing the transpiration surface progressively during the dry season, e.g. *Haplophyllum* and *Heliotropium*. They can support a big water-saturation deficit without damage. Their power of limiting transpiration is less than that of group (a), which is connected with the absence of xeromorphic characters, partly present in group (b).

4. *Atriplex.*

This plant forms a separate group. It loses its leaves very gradually, but differs from the herbaceous plants in that the power of limitation of transpiration is small. It resembles the ' sclerophylls ' in that transpiration is low. The water-saturation deficit of *Atriplex* is the largest attained by the plants examined.

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Root conditions of certain plants of the Wilderness of Judaea.

By MICHAEL EVENARI (WALTER SCHWARZ), F.L.S.

(With 11 figures in the text)

[Read 6 January 1938]

DURING the foregoing study of the transpiration of certain plants of the Judaean desert ('Journal of the Linnean Society', li, p. 323) it was found necessary to investigate the life-form of the roots of the plants. The following account embodies the results of investigations carried out on the plants listed below :—

ANNUALS.

- Linaria Haelava* (Forsk.) Chav.
- Erucaria Boveana* Coss.
- Aizoon hispanicum* Linn.

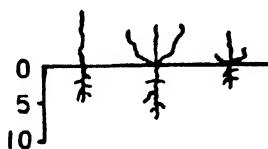
PERENNIALS.

- Haplophyllum tuberculatum* (Forsk.) Juss.
- Heliotropium rotundifolium* Sieb.

Reseda muricata Presl.

- Erodium glaucophyllum* Ait.
- Suaeda asphalctica* Boiss.
- Atriplex Halimus* Linn.
- Zygophyllum dumosum* Boiss.
- Retama Retam* (Forsk.) Webb.
- Salsola rigida* Pall.

Annuals.—The roots of the annuals of the Judaean desert are essentially the same as those of annuals of other habitats. They penetrate only a few centimetres into the soil and have very few secondary roots (see figs. 1–3). For *Erucaria* the maximum depth is 7 cm.

FIG. 1.—*Linaria Haelava* (left).FIG. 2.—*Erucaria Boveana* (centre).FIG. 3.—*Aizoon hispanicum* (right). All $\times \frac{1}{5}$.

Perennials.—Two types of root-system are shown by the perennials. *Suaeda*, a succulent plant, has a superficial root-system. Most of the other perennials show the same life-form ; they vary considerably as regards size and depth. The main root grows vertically for some distance before it forks. Side-roots grow horizontally from the main root, often covering a considerable area. Fine long absorbing roots grow from the horizontal roots.

Detailed description of the root-systems examined.

Suaeda (fig. 4).—The whole root-form of *Suaeda* is similar to that of the Cacti as described by Cannon (1911). The main root grows vertically to a

depth of 5 cm.: horizontal lateral roots radiate from this point covering a circle 2·2 m. in diameter (compare *Opuntia Artiuscula*, which penetrates 2 cm.).

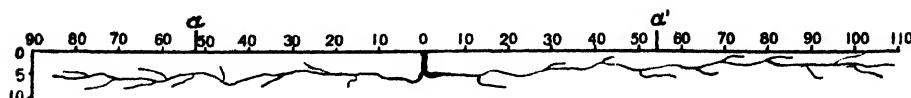


FIG. 4.—*Suaeda asphalctica*. $\times \frac{1}{10}$.

As *Suaeda* is a succulent plant Cannon's remark (1911, p. 67) 'the widely extending type of root is confined . . . to such as have water-storage capacity' seems to be justified.

Zygophyllum (fig. 5).—This has the most extensive root-system of the plants here described. The bush examined grew just above the edge of a Wadi. The root forked at 15–20 cm. below the surface and both branches had grown

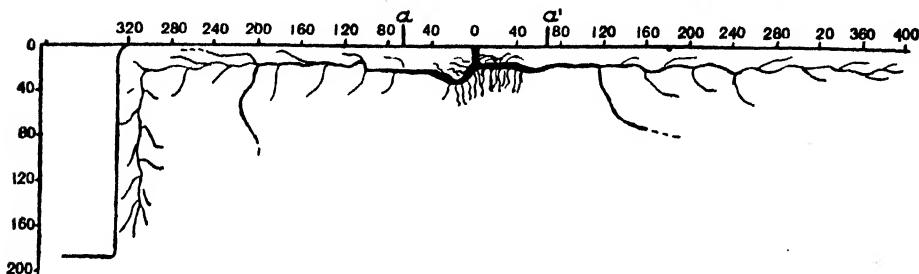


FIG. 5.—*Zygophyllum dumosum*. $\times \frac{1}{10}$.

parallel to the surface for a distance of 4 m. in one direction and 4·8 m. in the other. At the edge of the Wadi the root turned and followed the direction of the side of the Wadi, keeping the same distance from the surface. *Zygophyllum* like *Suaeda* belongs to Cannon's 'surface type', the root-system being typical of plants with water-storage capacity.

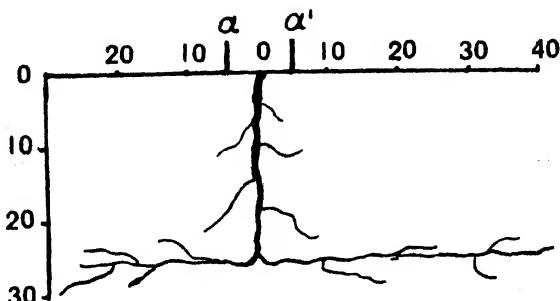


FIG. 6.—*Haplophyllum tuberculatum*. $\times \frac{1}{10}$.

Haplophyllum, *Heliotropium*, *Reseda*, and *Erodium* (figs. 6, 7, & 8).—These plants have the same type of root-system. The main root penetrates more

or less deeply into the soil, curves through a right angle to continue growing horizontally. In most cases at the point of curvature a lateral root arises, and like the main root grows horizontally but in the opposite direction. The root is therefore fork-like, the lateral and main roots being equal in size. In the figures the lateral extent of the shoot above ground is shown by the line $a-a'$.

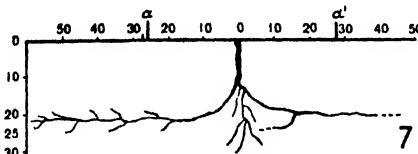


FIG. 7.—*Heliotropium rotundifolium*. $\times \frac{1}{20}$.

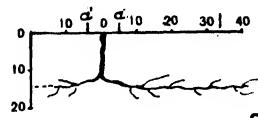


FIG. 8.—*Reseda muricata*. $\times \frac{1}{20}$.

Salsola (fig. 9).—The root-system is similar to those of the last plants described, except that the root bifurcates less abruptly.

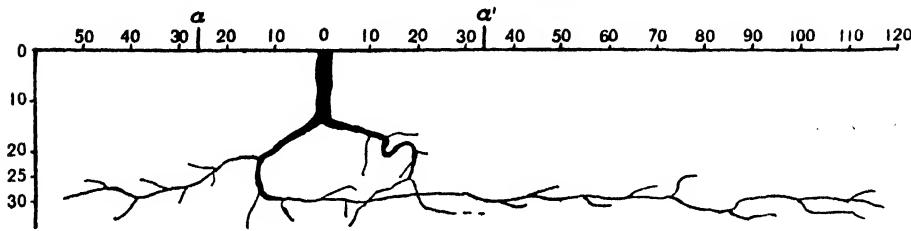


FIG. 9.—*Salsola rigida*. $\times \frac{1}{15}$.

Retama (fig. 10).—This plant has a somewhat different root-system from that described above. From the main root, but above the fork, numerous lateral roots about 3–5 m. long grow parallel to the surface at a depth of 5–10 cm. The main root itself forks at a depth of 10 cm. Each of the two

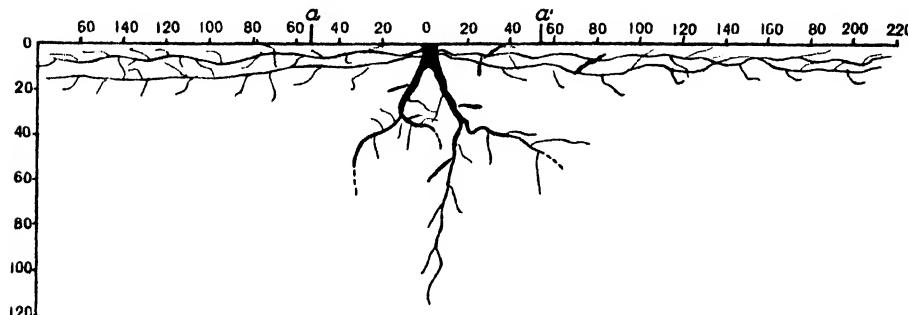


FIG. 10.—*Retama Retam*. $\times \frac{1}{35}$.

branches fork again. The thickest branch, which I followed to the end, penetrated to a depth of 1·1 m. This was the deepest root observed by me. According to Cannon the root-system of *Retama* shows a combination of 'the superficial and generalized types'.

Atriplex (fig. 11).—This is the only desert perennial examined by me which shows vegetative reproduction. It resembles in habit *Koerberlinia spinosa*, studied by Cannon in the Arizona desert. Both plants possess an underground stem which in *Atriplex* has a diameter of about 5 cm. and runs horizontally just below the surface of the soil. Aerial branches occur at intervals, and fine adventitious roots grow from the lower surface. From one end a root grows vertically to a depth of 50 cm., where it continues horizontally. The presence of either *Retama* or *Atriplex*, the deep-rooted plants, is a good indication of deep soil.

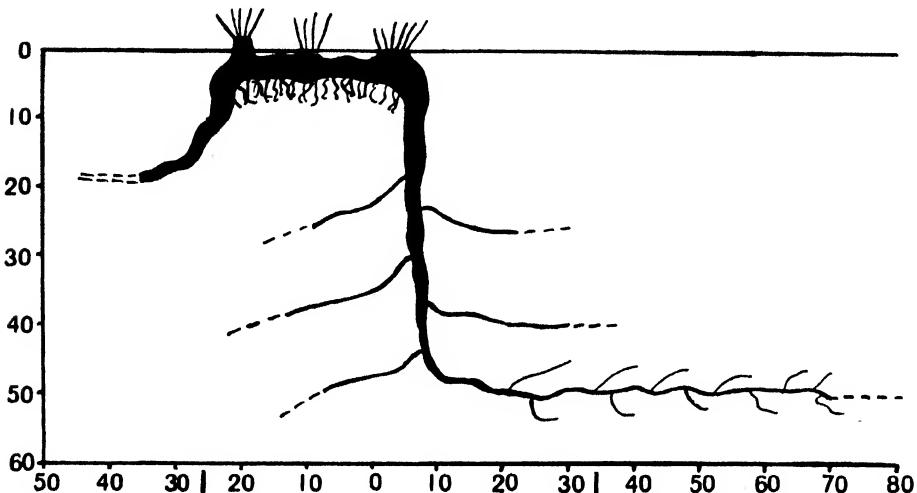


FIG. 11.—*Atriplex Halimus*. $\times \frac{1}{10}$.

Summing up these descriptions we may say that the main characteristics of these desert plants are :—

- (1) The roots penetrate only to a slight depth (excepting *Retama* and *Atriplex*).
- (2) The main root grows vertically, until it attains its maximum depth, whereafter it grows horizontally. At the curving point a lateral root is often found which grows horizontally in an opposite direction (except *Retama*). In our examples the behaviour is much more irregular than is to be inferred from Stocker's account.
- (3) The horizontal roots are comparatively long, especially those of *Zygophyllum* and *Retama*. This does not agree with Stocker's observations.
- (4) The extreme 'superficial type' of root is confined to the succulents.

*The mass development of the root, weight of the part above surface
quotient.*

Plant.	Determined on	
	Fresh weight.	Dry weight.
<i>Retama Retam</i>	5.75	..
<i>Haplophyllum tuberculatum</i>	3.33	2.12
<i>Heliotropium rotundifolium</i>	2.95	..
<i>Salsola rigida</i>	1.61	..
<i>Zygophyllum dumosum</i>	1.44	..
<i>Atriplex Halimus</i>	1.1	..
<i>Erodium glaucophyllum</i>	3.5	10.4
<i>Reseda muricata</i>	4.5
<i>Aizoon hispanicum</i>	17.1
<i>Linaria Haelava</i>	15.0
<i>Erucaria Boveana</i>	10.3

No figures for *Suaeda* are recorded in the Table as the unusual brittleness of the roots did not allow me to obtain them in a complete condition. My figures are much smaller than those of Stocker. The big-leaved herbaceous plants—Stocker's Group 2 a—have a value of 3.26, whereas his figure is 4.6. The succulents, for which I find a value of 1.44 (e.g. *Zygophyllum*), are given a value by Stocker of 110 to 21.2. My value for the annuals is very high: annuals have a small root-system by comparison with their shoot development.

I found an interesting fact in connection with *Erodium*, the fresh weight coefficient is 3.5, whereas the dry weight coefficient is 10.4. This big difference is due to the fact that the root bark is transformed into water-storing tissue from which drops of water can be pressed out even in May.

Summarizing, we may say that the mass development of the root-systems of our desert plants shows no special peculiarities and lies within the same limits as those recognized for other habitats. The root-systems show neither a stronger nor a weaker development than that given by Stocker for German species. My figures are too scanty for further deduction. The anatomical structure of the roots of the desert plants is as far as I have seen very peculiar and worth a thorough investigation.

The area occupied by the roots.

In my calculations the horizontal roots are only considered. The roots of *Retama* cover an area of 38 to 39 square metres. The roots of *Suaeda* 10 to 12 square metres. The other smaller plants cover an area of 1 to 2 square metres if, as Stocker does, the fine and very long suction roots typical of my plants are included.

I must agree entirely with Stocker when he denotes as a speciality of the root-system of desert plants 'die konkurrenzlose Bestreichung einer nach mitteleuropäischen Begriffen ausserordentlich grossen Bodenfläche und intensiven Aussaugung derselben', although the surface spread over, according to my calculations, is much bigger than according to Stocker, especially in the cases of *Retama*, *Suaeda*, *Salsola*, *Zygophyllum*.

The word 'incontestible' ('konkurrenzlos') used in the above sentence was confirmed by me in all my investigations; within the root area of any individual plant there was either not a single or only very few roots of any neighbouring species; this is quite contrary to the root picture which Weaver gives of the North American Prairie, where root competition plays an important part. Cannon recognizes, when he writes about the Algerian desert, that 'in the extreme deserts it is probable that the element of competition between the perennials, which is an important factor in the survival of a species in the moister region, is wholly lacking' (1911, p. 66).

The intensive exploitation of the surface used, about which we spoke, is made possible by the numerous fine suction roots which make their appearance in the wet season and which have also been noticed by Cannon.

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The physiological anatomy of the transpiratory organs and the conducting systems of certain plants typical of the Wilderness of Judaea. By MICHAEL EVENARI (WALTER SCHWARZ), F.L.S.

(With 16 figures in the text)

[Read 6 January 1938]

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DURING the course of the investigation of the water-balance of certain typical plants of the Judacan desert, described in this Journal, p. 323, the necessity of a knowledge of the anatomical structure of the transpiratory organs of these plants was realized. Such knowledge is also of general importance in the elucidation of many other problems of physiological anatomy.

Many of the plants (e.g. *Anabasis*) are of interest from the purely anatomical standpoint, but the main object of the investigation was the solution of the following problems :—

(1) How far can the various anatomical characteristics be summed up quantitatively, and how far is it possible to classify the plants investigated, with the help of these characters, into mesomorphs, xeromorphs, and succulents ?

(2) What connections exist between the structure and physiological function ? The main interest lies in the relation of the structure, position, and number of the stomata to the magnitude of the stomatal transpiration.

(3) The relationship between the structure and dimensions of the water-conducting system and the transpiration.

We now know that the structure of those organs through which water is transpired is not the only decisive factor in controlling the water output. It depends, also, on the structure of those organs through which the water flows to reach the place where transpiration occurs ; so that a knowledge of the water-conducting system and its dimensions is essential for a study of the water-balance. This paper is therefore divided into three parts. In the first part the anatomy of the transpiration organs of the experimental plants is

described, and the significance of the various anatomical characteristics from the point of view of xeromorphy and succulence is discussed. The second part contains calculations of the amount of water vapour which passes through the stomata of the various plants in unit time, from which an insight into the relation between structure and function is gained. The third part is devoted to calculations of the surface of the water-conducting system of the various plants and its relation to the transpiration.

The plants are again those used for measuring the transpiration (in the earlier paper just referred to). They are : *Reseda muricata* Presl, *Erodium glaucophyllum* Ait., *Heliotropium rotundifolium* Sieb., *Haplophyllum tuberculatum* (Forsk.) Juss., *Retama Retam* (Forsk.) Webb, *Atriplex Halimus* Linn., *Zygophyllum dumosum* Boiss., *Suaeda asphaltica* Boiss., *Salsola rigida* Pall., and *Anabasis articulata* (Forsk.) Moq.

ANATOMICAL STRUCTURE OF THE TRANSPIRATORY ORGANS.

A few of the plants investigated have already been described by Volkens (1887) in his atlas 'Die Flora der aegyptisch-arabischen Wueste'; and his data are referred to in the following account :—

1. *Reseda muricata*.—This perennial plant grows to a height of 30–50 cm. It has long leaves of various shapes, the lower undivided, the upper mainly tripartite. The leaf has an isolateral construction. The cuticle, which covers the large epidermal cells, is only slightly developed. The palisade-tissue passes without any sharp transition into the spongy mesophyll which is situated in the middle of the leaf and which is almost as green as the palisade-tissue itself. The intercellular spaces are numerous and well developed. The stomata (fig. 1) are like those described by Volkens for other desert species of *Reseda*, and are 'without any particular means of protection against loss by transpiration' (Volkens, 1887). The respiratory cavities are large, and apart from the 'water bladders', which are not very numerous, and the mucilage-cells, there are none of the customary xeromorphic characteristics.

2. *Erodium glaucophyllum* (fig. 2).—A perennial plant with a basal rosette of 10–15 large leaves which are mostly long-petioled. The outer walls of the epidermal cells of the isolateral leaf are not very thick, and are covered by a thin cuticle. The palisade-tissue consists of very long drawn-out cells. There is no definite spongy mesophyll. Intercellular spaces are present, but are not so plentiful as in the former species. The stomata are not deeply set; they have no cuticular ridges, and they show no xeromorphic characters.

3. *Heliotropium rotundifolium* (fig. 3).—A species which Volkens does not mention. This perennial plant bears on its branches long leaves with a felt-like hairy covering. The leaf is not quite isolateral in construction. The palisade-tissue of the upper surface consists of cells which are much more elongated than those of the under surface; and there is a clearly differentiated spongy mesophyll. The outer epidermal wall is not particularly thick. The epidermis has many large retort-shaped hairs, which narrow down suddenly

from a protuberant base into the actual hair. They constitute the very thick hairy felt, which is particularly well developed on the lower epidermis. The leaf has abundant intercellular spaces. The stomata show no xeromorphic characteristics.

4. *Haplophyllum tuberculatum* (fig. 4).—The leaves on the shoots of this perennial plant are of two types, which, however, are connected by intermediate forms. One type is 4–5 cm. long and very narrow, the other 1–1·5 cm. long

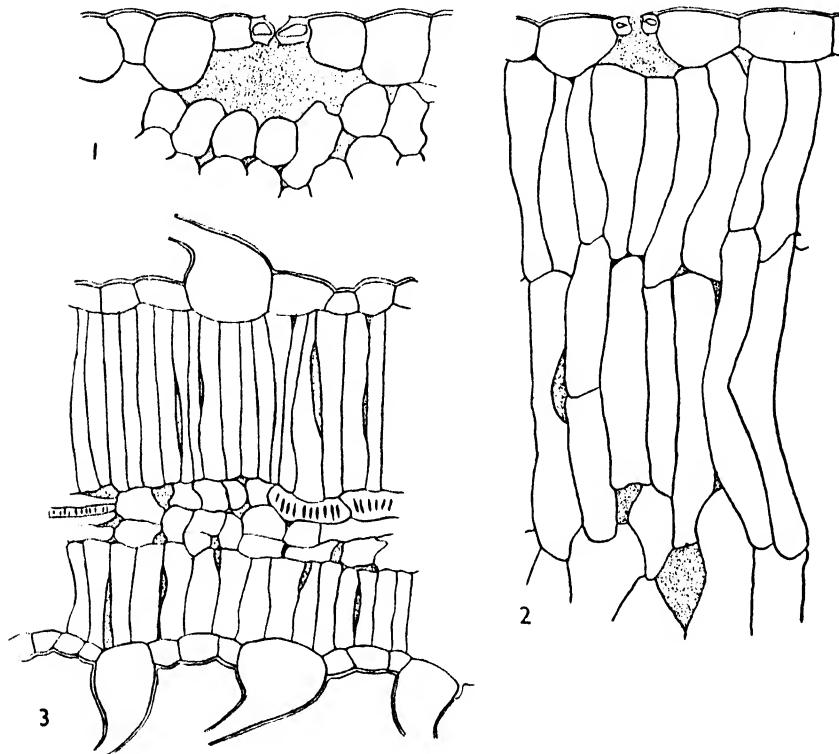


FIG. 1.—The upper surface of the leaf of *Reseda muricata*, in section, showing a stoma and the air-space below it.

FIG. 2.—The leaf of *Erodium glaucophyllum* in vertical section, upper part only.

FIG. 3.—The leaf of *Heliotropium rotundifolium* in vertical section.

and obovate in shape. The palisade-tissue on both surfaces is many-layered and passes gradually into the spongy mesophyll. The intercellular spaces in the palisade-tissue are not very well developed, but in the spongy mesophyll they are numerous and large. The stomata (fig. 5) are not deeply set, and the respiratory cavity is well developed. There are no hairs. In the leaf are situated glands which are filled with an etherial oil having a very unpleasant smell. These have been described by Volkens.

5. *Retama Retam*.—This leafless bush, which grows to more than the height of a man, shows in its branches a construction typical of xeromorphic plants. Along the branches there run a number of deep longitudinal grooves (fig. 6) in which the stomata are situated, and these grooves are more or less full of large hairs. A section taken across one of the protuberances between the grooves (fig. 6) shows in the middle a plate of sclerenchyma, bounded on either

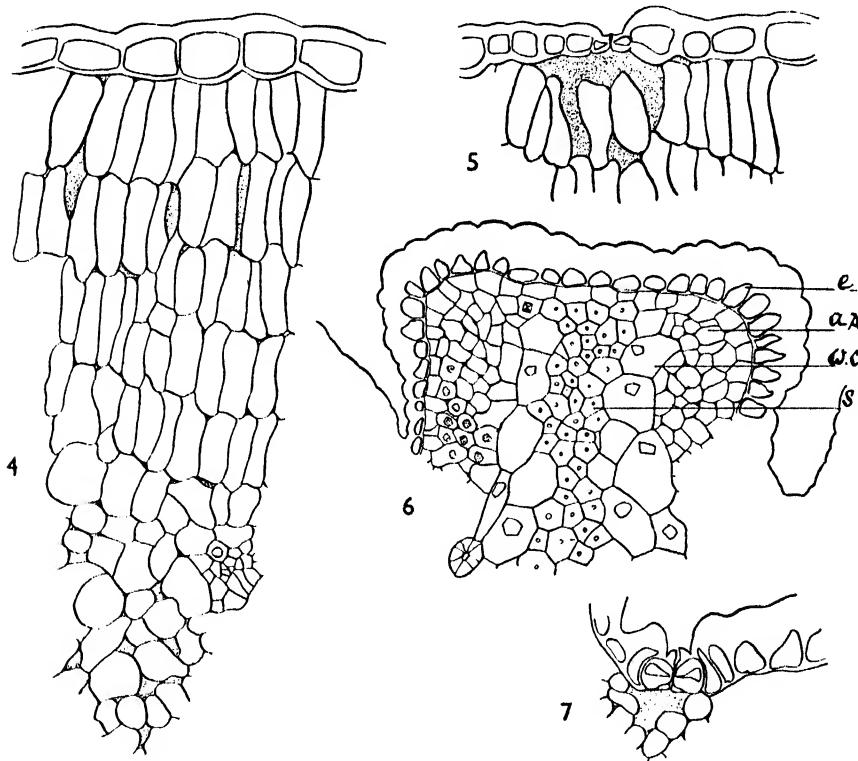


FIG. 4.—The leaf of *Haplophyllum tuberculatum* in vertical section, upper part only.

FIG. 5.—The stoma of the same.

FIG. 6.—One rib of the stem of *Retama Retam* in transverse section : *e.*, the epidermis ; *a.p.*, the assimilating parenchyma ; *w.c.*, the water cells ; and *s.*, the sclerenchyma.

FIG. 7.—A stoma of the same.

side by one or two rows of large colourless water-cells, most of which contain crystals. Outside these water-cells comes the assimilation parenchyma, consisting of small cells, each containing a single crystal (see fig. 6, wherein these crystals are only shown in a few cells). The epidermal cells have a very thick outer wall. The assimilation parenchyma has very few intercellular spaces. The stomata (fig. 7) are deeply set and have an outer and inner cuticular crest. The respiratory cavity is very small.

6. *Atriplex Halimus*.—The leaves of this large bush are of various shapes, about 2 cm. long, and show an isolateral construction. Beneath the epidermis, the outer wall of which is not very thick, is a layer of colourless isodiametric water-cells. The mesophyll is made up of green assimilatory cells which vary in shape, and large idioblasts containing crystals occur in various places.

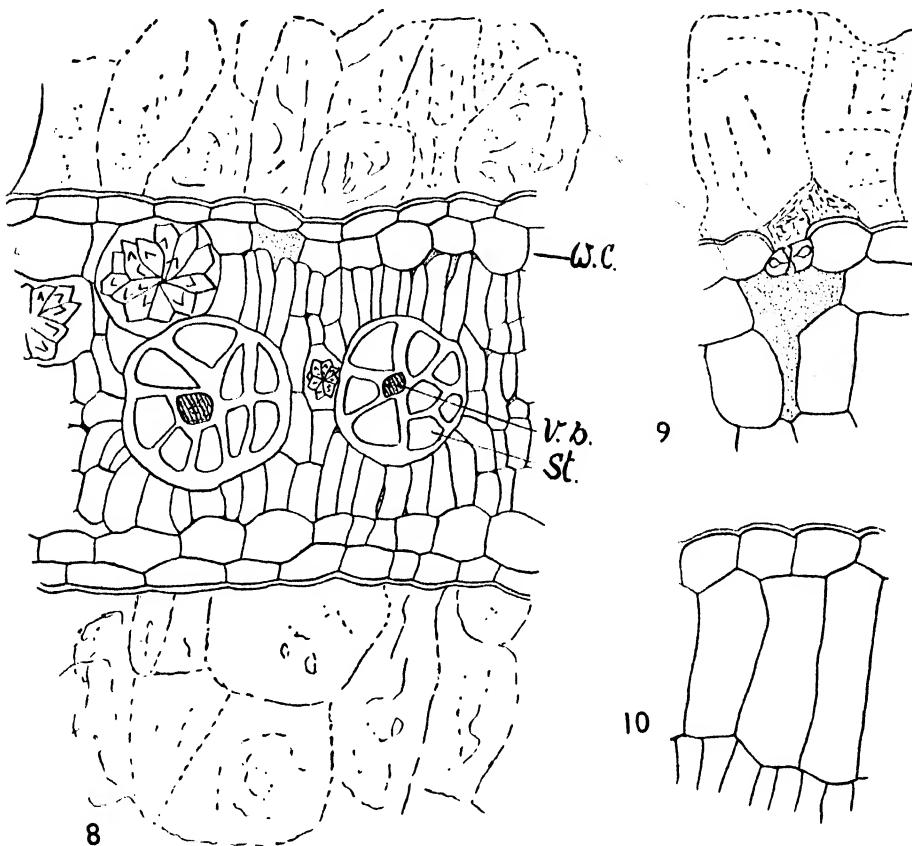


FIG. 8.—A leaf of *Atriplex Halimus* in vertical section, showing the remains of water-holding hairs above and below; *w.c.*, water-containing cells; *v.b.*, vascular bundle; *s.t.*, the surrounding tissue.

FIG. 9.—A stoma of the same.

FIG. 10.—Water-cells elongated as in spring.

Around each vascular bundle is a special zone of green tissue. Both upper and lower epidermis are covered with an almost complete layer of pseudo-tissue which is formed from the remains of bubble-like hair-cells. In the spring these cells are full of water, but later they collapse and give rise to this pseudo-tissue, a phenomenon which accounts for the extraordinary change of colour

which the leaves undergo in the course of the year. In the spring they are green, but in the summer, when the 'bubbles' dry up, their colour changes to a silver-grey. The stomata (fig. 9) are not deeply set, and the respiratory cavity is of medium size.

The colourless water-tissue is subject to large fluctuations in size with changes in the water-content of the leaf. Fig. 10 shows the water-tissue of a young leaf in spring, when there is sufficient water. Fig. 8 a is of a leaf in summer, and the tremendous difference in their size can easily be seen. The cell-walls

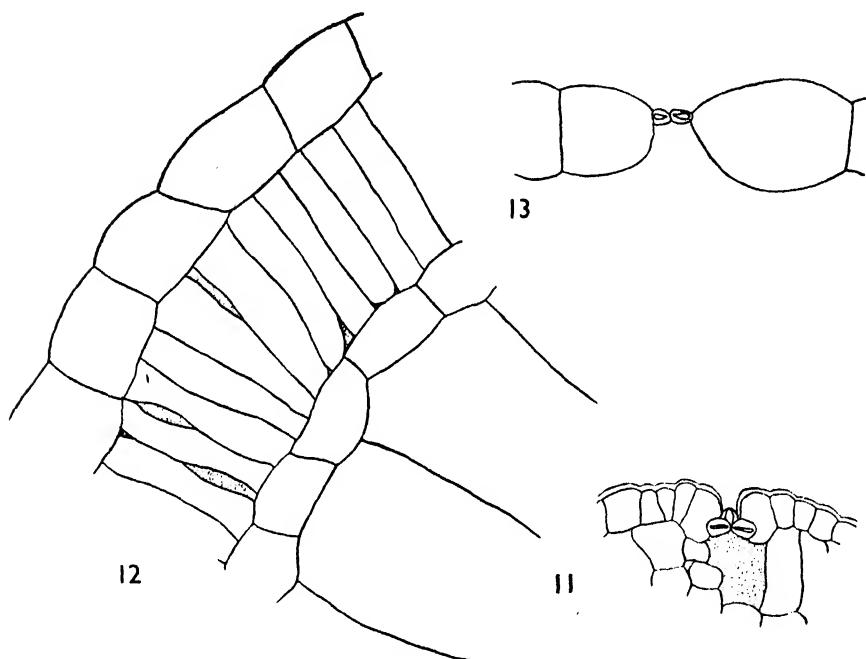


FIG. 11.—The stoma of *Zygophyllum dumosum*.

FIG. 12.—A small part of the surface of the cylindrical leaf of *Suaeda asphaltica* showing epidermis (above) with palissade-cells below it, then diagonal cells and (below) water cells.

FIG. 13.—The stoma of the same.

must be extremely elastic in order to contract from their 'spring-size' to their 'summer-size' without collapsing.

7. *Zygophyllum dumosum*.—A species not described by Volkens. The petioles are cylindrical and each bears two small leaflets, which are round or partially flattened. The outer epidermal wall is not specially thickened. Beneath the epidermis is a tissue composed of rather elongated green cells which passes without any sharp transition into the water-tissue in the centre of the leaf. This water-tissue is composed of very large, radially elongated

cells, many of which contain large crystals. The stomata (fig. 11) are fairly deeply set and have well-developed outer cuticular crests. The respiratory cavity is, on the average, smaller than that of the afore-mentioned plants, with the exception of *Retama*. There are no hairs.

8. *Suaeda asphaltica*.—A species not described by Volkens. This bush, which attains a height of about 1 m., bears in the spring cylindrical leaves 2–2.5 cm. long and full of sap. The epidermis is without hairs and its outer wall is not much thickened. Beneath the epidermis is a layer of elongated palisade-cells (fig. 12), and beneath this is a layer of diagonal cells. Between

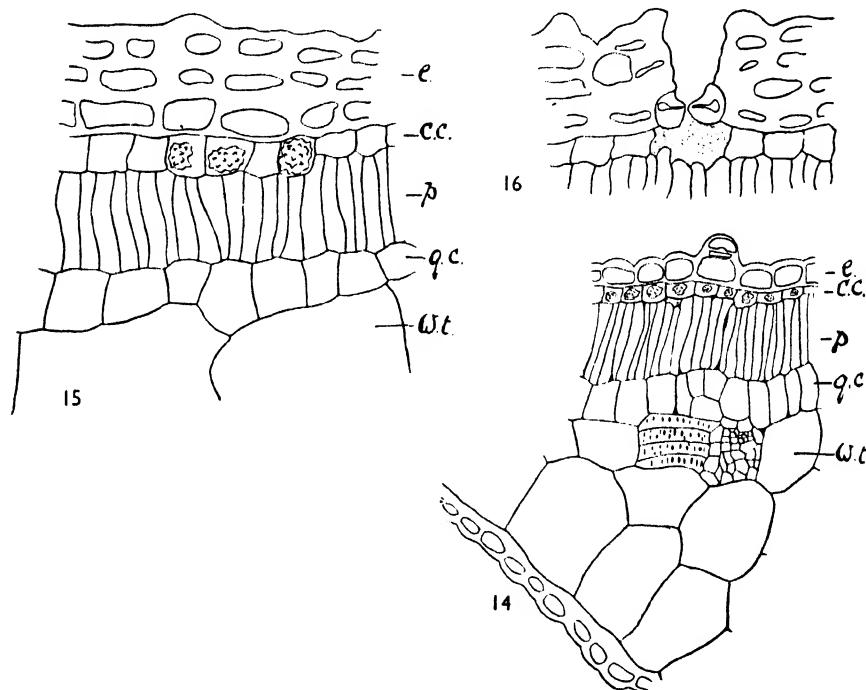


FIG. 14.—Part of a sickle-shaped leaf of *Salsola rigida*.

FIG. 15.—Part of the stem of *Anabasis articulata*.

FIG. 16.—A stoma of *Anabasis*: e., epidermis; c.c., cells with crystals; p., palisade-tissue; q.c., quadratic cells; and w.t., water-tissue.

this layer of diagonal cells and the central vascular bundle is a layer of very large water-cells, arranged radially. The stomata (fig. 13), which are very small in comparison with the epidermal cells, are not set very deeply.

9. *Salsola rigida*.—A species not described by Volkens. A bush 1–1½ m. high bearing small scale-like leaves. At the base the leaves are sickle-shaped in cross-section, but towards their apex they are round. The following description applies to the base. The lower epidermis has a very thick outer

wall and below it there is a layer of colourless quadratic crystal-bearing cells (fig. 14) without intercellular spaces. Further inwards is the green palisade-tissue, and below this a layer of more or less quadratic cells deep green in colour. Between this and the upper epidermis is the large-celled water-tissue. The cylindrical apices of the leaves differ in their radial construction. The crystal, palisade, and quadratic cells are not confined to the lower surface, but occur all round the leaf. The leaf has few intercellular spaces.

10. *Anabasis articulata* (Volkens, 1887, p. 140).—A leafless bush attaining a height of about half a metre. The young green internodes have three-layered epidermis, the cells of which are very thick-walled (fig. 15). Under the epidermis, as in *Salsola*, there is a layer of crystal cells and beneath this a palisade-layer. Still further inwards occurs a layer of green quadratic cells and in direct connection with this an extensive water-tissue. These outer tissues are separated from the central vascular bundle by a cork layer, and, as Volkens states, the only connection between them is by radial ramifications of vascular tissue. In older branches, however, these ramifications are also traversed by the cork layer, so that all the outer tissues eventually dry up and are shed in strips from the central part which continues to increase in thickness. The young shoots of the present year thus appear to be grafted on to the older hardened shoots of the previous year. This phenomenon of two shoots, entirely different in their construction, with one growing inside the other, should repay further investigation. The stomata (fig. 16) are very deeply set. The respiratory cavity is very small, and the intercellular spaces are very poorly developed.

From the anatomical descriptions given above it appears that there are certain characteristics common to all the plants described, and these features will now be discussed, special stress being laid on the so-called xeromorphic structures. The word 'xeromorphic' is here used in a purely descriptive sense, as Firbas uses it, and not in the old physiological-anatomical sense. Whether in fact there is any connection between the physiology and the anatomy of these structures will be discussed in a later section.

Firbas (1931, p. 482) regards the following structures as 'xeromorphic':—

- (1) Thickening and cutinization of the epidermal wall.
- (2) Coverings of wax and thick hair.
- (3) Depression of the stomata, and overarching of the cuticle, or the sinking of the surface containing the stomata into grooves, sometimes covered with hair.
- (4) Interception of tightly-pored hypodermic plates under the stomata.
- (5) Reduction in the size of the leaves and the consequent shortening of the passage between the transpiring cells and the main water-conducting system.
- (6) Mechanical fixing, particularly of the water-conduits.

I do not include in this scheme Firbas's fourth characteristic, namely, 'formation of the water-tissues'.

The herbaceous species, of the genera *Erodium* and *Reseda*, show none of these characteristics. The herbaceous *Heliotropium* shows character no. 2; *Haplophyllum* characters nos. 1, 3, and 5. The large-leaved *Atriplex* shows characters nos. 2 and 3, and the broom-like *Retama* characters nos. 1, 2, 3, and 6. *Anabasis* shows characters nos. 1, 3, and 6. In both *Retama* and *Anabasis* character no. 5 is extremely well developed, and they are both entirely without leaves. *Salsola* shows characters nos. 1 and 5, *Zygophyllum* nos. 1 and 3.

The succulents, on the other hand, show different anatomical characteristics. The following is a list of the most important :—

- (7) Strong development of the water-tissues.
- (8) Slight development of the top-surfaces.
- (9) The mechanical elements entirely lacking or only slightly developed.
- (10) Slight development of the water-conducting system.
- (11) Thin outer epidermal walls (?).

Suaeda shows all of these characteristics, *Zygophyllum* nos. 7 to 10, *Salsola* nos. 7, 9, and 10, *Anabasis* no. 7, and *Atriplex* nos. 7 and 10.

On the basis of these characters the plants investigated can be arranged in the following groups, according to their anatomical structure :—

- i. Extreme xeromorphic :—*Retama Retam*.
- ii. Herbaceous with a few xeromorphic characteristics :—*Heliotropium rotundifolium*, *Haplophyllum tuberculatum*.
- iii. Non-herbaceous xeromorphic with succulent characteristics :—*Anabasis articulata*, *Salsola rigida*.
- iv. Herbaceous with a few succulent and xeromorphic characteristics :—*Atriplex Halimus*.
- v. Herbaceous without xeromorphic characteristics :—*Erodium glaucophyllum*, *Reseda muricata*.
- vi. Full succulents :—*Suaeda asphaltica*.
- vii. Succulents with xeromorphic characteristics :—*Zygophyllum dumosum*.

The isolateral construction of the leaf is also a characteristic common to all plants investigated, except those without leaves. Stocker (1928, p. 787, and 1933, p. 11) says that the tendency to an isolateral construction is very frequent in habitats where the light intensity is high, an observation which is entirely confirmed by the present investigation. The sizes and numbers of the stomata in the various plants, are given in Table I, from which these relations appear :—(A) In all the leaves the upper surface has more stomata than the lower one. This also may be a feature characteristic of plants growing in a strongly lighted habitat. (B) The highly succulent species differ from the non-succulent or slightly succulent species in having a smaller number of stomata. *Atriplex Halimus*, however, which shows certain succulent features, has a large number of stomata. *Reseda muricata* in respect of this feature is midway between the succulents and non-succulents. (C) The length of the

TABLE I.—Number and size of stomata.

Plant.	Number of stomata per square mm. Upper surface.	Number of stomata per square mm. Lower surface.	Length of guard- cells.	Length of fissure.	Thickness of outer walls of epidermis.
<i>Haplophyllum tuberculatum</i>	184	165	36 μ	20.6 μ	8-10 μ
<i>Atriplex Halimus</i>	151	127	30 μ	14.8 μ	3-3.5 μ
<i>Heliotropium rotundifolium</i>	145	130	26.4 μ	13.2 μ	3-4 μ
<i>Erodium glaucophyllum</i>	126	115	27 μ	13.2 μ	3-4 μ
<i>Reseda muricata</i>	82	61	38.9 μ	18 μ	2-3 μ
<i>Suaeda asphalctica</i>	58	..	45 μ	23 μ	0.5-1 μ
<i>Anabasis articulata</i>	39	10-14 μ
<i>Zygophyllum dumosum</i>	37	37	41 μ	23 μ	3-4 μ
<i>Retama Retam</i>	20-25 μ

guard-cells and of the stomatal passage vary inversely with the number of stomata. The only exception is *Haplophyllum tuberculatum*, which has a large number of stomata and also has very long guard-cells. The stomatal passage in this species is also exceptionally long; and, although it is smaller than those of the succulents, it is larger than that of *Reseda muricata* with its small number of stomata.

TABLE II.—From Firbas (1) and from Salisbury (2-4)
(see Firbas, 1931).

Groups of plants.	Number of stomata per square mm. Upper and lower surfaces.
Xerophytes of the desert, non-succulents	129
Bog-plants (1)	114
Plants of border of forests, England (2)	83
Water and swamp-plants (3)	61
Shade-plants of British forests (4)	46
Succulents of desert	45

In conclusion, we may say that the herbaceous plants with xeromorphic characteristics have the greatest number of stomata, and that herbaceous plants without xeromorphic characteristics have a smaller number. The type with the fewest stomata per unit area are the succulents. Comparing these figures with those of plants from other types of vegetation (Table II)

we see that the non-succulent desert xerophytes show the highest stomatal numbers of all. The desert succulents, on the other hand, show the lowest values.

THE TRANSPIRATION THROUGH THE STOMATA.

In order to appreciate the effectiveness of the stomatal apparatus and in order to see what relations, if any, exist between the structure of the stomata and their physiological activity, the study of their anatomical construction is not in itself sufficient. Conclusions as to physiological activity must not be drawn from mere outward appearances as was at one time the fashion in physiological anatomy. In order to see what effect the structure of the stoma has on the transpiration one must know how much water-vapour passes through the same number of stomata in the various plants in the unit of time under similar conditions of evaporation. Such a calculation is here possible, as transpiration measurements have been carried out over the course of a year on the same plants whose physiological anatomy has been described above. The result of this calculation is drawn up in Table III, the figures being taken from the earlier publication entitled 'Physiological-ecological investigations in the wilderness of Judaea' (this journal, p. 323). In the table is given the number of mg. of water-vapour given out by 1000 stomata during the course of the day, and in addition the number of mg. given off per minute by 100,000 stomata when transpiration was at a maximum for that particular day. Both calculations were necessary for the following reasons:—if calculations were only made of the total amount of water transpired during the day, occasions might arise where this total was very small, although over the short-lived period of maximal transpiration the stomata were heavily burdened. In such a case conclusions based solely on a knowledge of the daily total would be entirely misleading. *Retama Retam* is unfortunately missing from the table, because it was found to be impossible to estimate, even approximately, the number of stomata per unit area on its surface. It is quite certain, however, that its stomatal number is less than in *Anabasis articulata*. Its transpiration, on the other hand, exceeds that of *Anabasis*, so that there can be little doubt that *Retama* heads the list with regard to the amount of water given out per stoma.

It can be seen from the table that the stomata of *Anabasis articulata* (and also those of *Retama Retam*), which are of extreme xeromorphic construction, are amongst those which pass the largest amount of water-vapour in unit time. The absolute maximum is shown by *Anabasis*, and on one day only was it exceeded by *Reseda* in the total amount of water-vapour passed. The achievement of these stomata on a day such as 18. vii. 34, when the conditions were extreme, is quite astonishing. *It is therefore established beyond doubt that both average and maximal values of the transpiration per unit number of stomata are greater in the xeromorphic xerophytes, with their so-called 'protective' adaptations, than in the xerophytes which lack such features.*

TABLE III.—First column of each pair, mg. water given out by 1000 stomata per day.
 Second column, mg. water by 100,000 stomata per minute at the time of the maximal transpiration.

Date	14. ii. 34.	20. iii. 34.	30/31. v. 34.	26/27. vi. 34.	4. viii. 34.	29. ix. 34.	24. xi. 34.
Plant.	Per day.	Max.	Per day.	Max.	Per day.	Max.	Per day.
<i>Haplophyllum</i>	29.3	3.42	48.0	5.43	6.35	1.89	14.2
<i>Reseda</i>	34.1	5.63	66.0	10.2	13.3	3.96	..
<i>Heliotropium</i>	15.8	2.83	11.3	3.49	10.35	2.15	15.8
<i>Atriplex</i>	1.37	0.49	3.06
<i>Erodium</i>	29.0	4.45	19.3	4.85	15.4	3.48	..
<i>Zygophyllum</i>	19.7	3.97	9.9	3.16	13.7	3.03	..
<i>Suaeda</i>	5.09	1.20	8.06	2.29
Date	26. iv. 34.	18. vii. 34.					
<i>Anabasis</i>	56.7	12.1	35.2	8.5			

This must not be taken to mean, however, that such structures are without significance, because we have no means of telling what the transpiration of these plants would be had they not got these 'protective' structures. Comparison between various plants of the same habitat only shows us that these structures do not endow those plants which bear them with any superiority over their neighbours with regard to the amount of water given out per stoma, i.e. they have no greater economy of the water-balance. Even in the light of these observations, however, these structures do not appear to be entirely without effect. Although the transpiration through each individual stoma is greater, it has often been observed that such plants possess the property of being able to cut down their transpiration to zero very suddenly, and it is probable that this effective closing of the stomata is largely due to their position and structure. In addition, the cuticular transpiration of these xeromorphic plants is very low. The lowest values in the table are shown by *Atriplex Halimus* and not by the full succulents. This astonishing result is no doubt due to the protection afforded by the peculiar 'pseudo-tissue' of water- or air-filled cells with which the leaf of *Atriplex* is covered. The full succulents, at least in the case of *Suaeda asphaltica*, show low transpiration-values, in spite of their low number of stomata per unit area, the large size of the individual stomata, and the lack of any kind of protective apparatus. In the opinion of the author the low stomatal transpiration of succulents is connected with the poor development of the intercellular space system.

The behaviour of *Zygophyllum dumosum* on 30. iii. 34 is of great interest, as its transpiration per stoma was actually greater than that of either *Reseda muricata* or *Haplophyllum tuberculatum*. The transpiration of *Haplophyllum* was greatly reduced on that day; but it appears that the stomata of *Zygophyllum* and of full succulents in general have not the power of cutting down their transpiration to any great extent when this becomes necessary. During the course of each day on which measurements were made, although the fluctuations were here small, it was observed that the stomatal movements of the succulents, especially of *Suaeda*, were slow.

The former statement regarding the low transpiration of succulents therefore requires further qualification. The intensity of their transpiration per stoma in comparison with other plants is low only on days when the water-supply is plentiful. When the water-supply from the soil is poor, their transpiration is high relative to that of other types of plants, as they apparently lack the power of adapting themselves to such conditions.

This probably accounts for the short life of the leaves of *Suaeda*. These were the shortest-lived organs of any of the plants examined, including even the annuals. It also probably accounts for the fact that the succulents, at least in this habitat, discarded their leaves during the dry season.

Of the herbaceous plants the lowest values of transpiration per stoma are shown by *Heliotropium rotundifolium*, although this plant takes second place

in the list when transpiration per unit of fresh weight is considered. Its stomata, however, show no particular 'protective adaptations'. Its leaves, on the other hand, have a thick felt-like covering of hair, which apparently, as in the case of *Atriplex*, helps to limit the transpiration. The herbaceous plant with the greatest transpiration per stoma is *Reseda muricata*. For transpiration calculated on a fresh-weight basis, however, the highest values are shown by *Haplophyllum tuberculatum*. This is accounted for by differences in stomatal number. *Haplophyllum* shows the maximum number of stomata per unit area, and *Reseda* has a much smaller number, so that, for an equal quantity of water-vapour transpired, the individual stomata of *Reseda* must transpire more than those of *Haplophyllum*.

THE TRANSPERSION AND THE WATER-CONDUCTING SYSTEM.

For the investigation of the water-balance of these plants some knowledge of the water-conducting system was indispensable. It is to-day possible by Huber's method (1923, 1924) to calculate exactly the dimensions and the efficiency of the water-conducting system.

The majority of the figures given here, with the exception of those for *Anabasis articulata* and *Retama Retam*, refer to the water-conducting system of the petioles for the following two reasons :—

(1) The transpiration measurements were usually made on individual leaves, and information was required as to the water-conducting system of these same leaves.

(2) The variations in the dimensions of the water-conducting system from leaf to leaf are less than those which occur in the stem from base to apex. This observation was made by Firbas (1931), and has been confirmed by the writer.

In Table IV are given the values of the ratios c/w

$$\left(= \frac{\text{surface of water-conducting elements}}{\text{fresh weight of organ}} \right)$$

and c/s $\left(= \frac{\text{surface of water-conducting elements}}{\text{surface of organ}} \right)$.

With regard to the c/w values the highest values are shown by *Heliotropium rotundifolium* and *Haplophyllum tuberculatum*. Then follow *Reseda muricata*, *Retama Retam*, *Atriplex Halimus*, *Erodium glaucophyllum*. In the case of the c/s values the sequence is *Heliotropium*—*Haplophyllum*—*Retama*—*Atriplex*—*Erodium*—*Reseda*. In both cases *Heliotropium* and *Haplophyllum* show the highest values. *Anabasis*, *Salsola*, *Suaeda*, and *Zygophyllum*, on the other hand, show very low values for c/w and c/s ratios.

In general, we may say that these ratios are roughly proportional to the intensity of transpiration. This is true in the extreme cases of *Heliotropium* and *Haplophyllum* on the one hand and *Suaeda* and *Zygophyllum* on the other. *Atriplex*, however, shows much higher values of relative conducting surface

TABLE IV.— c/w or $\frac{\text{surface of water-conducting elements}}{\text{fresh weight of organ}}$, t/c or $\frac{\text{surface of water-conducting elements}}{\text{surface of water-conducting elements}}$, transpiration,
 c/s or $\frac{\text{surface of water-conducting elements}}{\text{surface of organ}}$, etc.

	c/w $(\frac{\text{mm.}^2}{g})$.	t/c $(\frac{g}{\text{mm.}^2})$.	c/s $(\frac{\text{mm.}^2}{\text{dmr.}^2})$.	V.	$t:c$ $\frac{\text{V.}}{\text{mm.}^2}$.	c/w (shoot).	No. of tracheids per mm. ² .	Medium lumen of tracheids in μ^2 .	Number of tracheids.	Medium lumen of tracheids.	Percent. of lumen.	V. of shoots.
<i>Anabasis</i>	0.0704 (0.750)	6.6	0.52	6.83	0.97	..	3090	37	11.43
<i>Heliotropium</i> ...	1.626	1.52	6.2	13.0	0.117	2.4	1248	79.9	9.97	412	661	27.2
<i>Haplophyllum</i> ...	0.967	2.4	4.53	11.9	0.22	1.36	2430	55.2	13.4
<i>Erodium</i>	0.317 (0.65)	5.16	1.26 (3.38)	162.5	0.032	..	1490 (135)	261.6 (658)	38.038 (8.9)	947	456	43.2
<i>Suaeda</i>	0.073	11.58	0.244	12.6	0.92	..	1530	71.7	11.0
<i>Salsola</i>	0.112	6.06	..	14.48	0.42	0.333	2280	56.8	12.95	1695	136.2	23.1
<i>Retama</i>	0.438 (0.53- 0.38)	1.54	1.76	58.8	0.026	..	1205	174	20.9
<i>Atriplex</i>	0.353	2.35	1.69	3.88	0.61	..	2020	34.5	6.95
<i>Zygophyllum</i> ...	0.116	2.40	0.47	12.83	0.19	0.493	4090	44.2	18.05
<i>Reseda</i>	0.463	4.9	0.905	101.5	0.048	..	2050	174.7	35.9
<i>Petiole (ex. <i>Anabasis</i> and <i>Retama</i>).</i>												Stem.

than would be expected from its low intensity of transpiration. In the case of *Anabasis*, on the other hand, the values of relative conducting surface are smaller than would be expected from its transpiration intensity.

The value of the relative conducting surface does not give any exact information as to the physiological achievement of the conducting system, and for this reason the quotient t/c (=transpiration/surface of water-conducting elements) was calculated. The values are given in Table IV. In the calculation the maximum value of t observed during the experimental year was used, so that the quotients represent the maximum achievement of the conducting system of each species. (The transpiration-values were taken from the paper entitled 'Physiological ecological investigations in the wilderness of Judaea').

The most heavily burdened conducting system is that of *Suaeda*, in spite of the low intensity of transpiration in this plant. *Zygophyllum* shows a much lower value, so that the succulents are by no means a uniform group in this respect. The same may be said of the extreme xeromorphic types. *Retama* shows an extraordinarily low value for its t/c ratio and *Anabasis* a much higher one. The herbaceous plants, also, do not show any uniform behaviour, although they tend to show low values. The index of conductivity (v) was calculated according to the method of Huber and is given in Table IV. The highest values are found in the case of *Erodium* and *Reseda*, that of *Retama* is lower and *Atriplex* shows the lowest value. The indices of *Heliotropium* and *Haplophyllum*, the species with the highest intensity of transpiration, are very small. As was observed in the case of the t/c quotient, the index of conductivity bears no definite relationship to the intensity of transpiration. It must, however, be added that these indices cannot be regarded as a reliable measure of the actual conducting force; for, as Berger has shown, the actual values of this force deviate 10 to 100 per cent. from the calculated values. It is therefore questionable whether any comparisons based on the figures given in the table are justified.

We also require to know the resistance per unit length which the conducting system offers to the transpiration stream. This is given by the quotient tc/V , the values of which are given in Table IV. The lowest resistance is shown by *Retama* and the highest by *Anabasis*. Both these plants show xeromorphic characteristics, so that here again we have an example of variation in physiological behaviour within a group. A comparison of the resistances of *Suaeda* and *Zygophyllum* provides a further example.

In conclusion, a summary of the chief characteristics of the conducting systems of the various species is given:—

1. *Retama Retam*.—Wide tracheids; medium lumen percentages; small number of tracheids; medium to large relative conducting surface; great conducting force; very small requirement; minimal resistance. In other words, an 'advantageously' constructed conducting system.

2. *Anabasis articulata*.—Very narrow tracheids; maximal number of

tracheids ; small lumen percentage ; minimal conducting force ; big requirement ; maximal resistance. In all these points we have the exact opposite of what we find in *Retama*, although on the basis of other relations we must include these two plants in the same group. The difference in the construction and achievement of their conducting systems is probably due to the fact that the anatomical construction of *Anabasis* shows succulent as well as xeromorphic characteristics, whereas the former are entirely lacking in the case of *Retama*. It is possible that the presence of water-reservoirs in *Anabasis* (with the biggest w/s quotient) renders the possession of a well-developed and promptly acting conducting system superfluous. *Retama*, on the other hand, which has the lowest water-reserve, is dependent on a much prompter action of the water-conducting system.

3. *Suaeda asphaltica*.—Medium width tracheids ; small number of tracheids ; small to medium lumen percentage ; smallest conducting surface ; low conducting force ; maximal requirements ; biggest resistance. On the whole, a heavily burdened and 'unfavourably' constructed system.

4. *Zygophyllum dumosum*.—Small tracheid-lumen ; maximal number of tracheids ; medium lumen percentage ; small conducting force ; small requirement ; small conducting surface ; low resistance.

5. *Heliotropium rotundifolium*.—Medium tracheid-lumen ; small lumen percentage ; small number of tracheids ; the highest conducting surface ; slight conducting force ; smallest requirements ; medium resistance.

6. *Haplophyllum tuberculatum*.—Small tracheid-lumen ; medium number of tracheids ; medium lumen percentage ; low conducting force ; large relative conducting surface ; small requirement ; medium resistance.

7. *Erodium glaucophyllum*.—Maximal lumen ; maximal lumen percentage ; small number of tracheids ; medium conducting surface ; maximal conducting force ; medium to large requirements ; very low resistance.

8. *Reseda muricata*.—Big lumen ; medium number of tracheids ; big lumen percentage ; medium conducting surface ; big conducting force ; medium requirement ; small resistance. *Reseda* and *Erodium* therefore resemble each other closely in these respects.

9. *Atriplex Halimus*.—Smallest lumen ; medium number of tracheids ; lowest lumen percentage ; lowest conducting force ; medium conducting surface ; small requirement ; high resistance.

10. *Salsola rigida*.—Smallest lumen ; medium to large number of tracheids ; medium lumen percentage ; small conducting surface ; low conducting force ; medium to large requirement ; medium resistance.

If we now cast a final glance through this list we see clearly that, apart from the relative conduit surfaces, there exists no relationship between transpiration intensity and the anatomy of the conducting system.

From these considerations we come to the following conclusions :—The whole group of herbaceous species showing a high intensity of transpiration have a medium or low resistance, and within this group the resistance is

inversely proportional to the intensity of transpiration. The two plants of this group which show the lowest transpiration intensity also show the highest conducting force, and the two with the highest transpiration the lowest conducting force.

The value of the requirement shows much variation within the group, but in general we may say that the plants with the highest intensity of transpiration have the lowest requirements.

In the case of the xeromorphs and the succulents these relationships are still more obscure.

Investigation also shows that no definite relations exist between the intensity of transpiration and the magnitude of the quotient w/d , which is the water-content per unit of dry weight, although on *a priori* grounds we might have expected such a relationship to exist.

If the values given in this paper for the medium tracheid lumen and the conducting surface are compared with those given by Stocker (1928) and Firbas (1931), it will be seen that certain discrepancies exist. Our values are smaller in the case of the medium tracheid lumen, but larger in the case of the number of tracheids and the lumen percentage, than the values given by these writers. In the case of *Erodium* the values given by Stocker are entered in brackets in Table IV.

These discrepancies are to be accounted for by the fact that the results here given refer to the petioles, whereas both the other writers examined whole leafy shoots. According to a letter which I received from Professor Huber all investigators unanimously agree 'that the elements in the petioles are narrower, the conducting powers therefore correspondingly smaller and in many cases the conducting surfaces also smaller, than in the corresponding stalk'. Added to this is the fact that the number of tracheids in the petioles is larger than that in the stalk. In order to confirm these observations measurements were made on short portions of the stem as well as on the petioles of several of the plants (see Table IV). The relative conducting surface, tracheid lumen, and conducting force were found to be larger than in the petioles, whereas the number of tracheids was smaller. The lumen percentage, on the other hand, was larger in the stem than in the petioles, so that this does not account for the much lower figures given by Stocker.

The calculation of the indices of conducting force in the stem give interesting results. The ratio between the conducting forces of *Heliotropium* and *Erodium*, for example, is 1/12.5 in the petiole, but only 1/1.09 in the stem. We see, therefore, that the relationships of the various dimensional quotients to each other are different in the stem and in the petiole, and this might possibly explain why I have been unable to establish any relationship between the intensity of transpiration and the construction of the water-conducting system. It may be that such relationships do actually exist, but that in the petiole they are concealed by the 'Vorschalt-Widerstände' factor of the German authors. This problem should be subjected to a further careful investigation.

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(PLATES 24-31, and, in the text, 6 maps and 21 figures)

[Read 7 May, 1936]

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THIS paper does not claim to be more than a working account of the wild and cultivated species and forms of *Epimedium* and *Vancouveria*. These plants have long been confused in gardens, and previous revisions of the group were found to be inadequate and sometimes quite misleading when applied to the kinds cultivated in the University Botanic Garden at Cambridge, England, where this paper was prepared in 1932 *.

To understand the garden plants and to correct their nomenclature it was necessary first to consider them in relation to wild species. This involved a critical study of the literature and herbarium material and of many living plants. This revision of the whole group is the result. The 'dire tangle' of the cultivated Epimediuums prompted Adrien Franchet and J. G. Baker to the same task.

Aceranthus is here treated as a subdivision of *Epimedium*, but *Vancouveria* as a separate genus. The whole group corresponds to Spach's *Berberideae*—*Epimedineae*, and belongs to the *Berberidaceae*, subfamily *Berberidoideae*, tribe *Epimedieae* of Engler. 'Epimedium sensu lato' in the following pages refers to this whole group; 'Epimedium', unqualified, to the dimerous Old World group (*Epimedium*, § *Euepimedium* Franch.) with the trimerous American

* Since then various additions have been made as the increase of knowledge demanded.

group *Vancouveria* excluded. The present paper describes three species of *Vancouveria* and twenty-three species of *Epimedium*, with ten subordinate categories and eleven horticulturally distinct plants of supposed hybrid origin. By adopting a slightly different view-point, twenty-seven species (four of which are here treated as subspecies) could reasonably be recognized. Although numerically much inferior to the shrubby genera *Berberis* (with about 240 species) and *Mahonia* (with about 65), *Epimedium* is the largest genus of herbaceous Berberidaceae. Twenty-three varietal and specific names have been applied to *Vancouveria*, 136, including those published here, to *Epimedium*.

It is my pleasant duty to acknowledge the help received from institutions and individuals, to all of whom I would tender my best thanks. For the loan of herbarium material I am under great obligation to Prof. L. Diels, Botanisches Museum, *Berlin-Dahlem*; the Botanische Anstalten, Universität, *Breslau*; the Moravské Zemské Museum, *Brno*; Prof. Kalipada Biswas, Royal Botanic Garden, *Calcutta*; Mr. S. C. Simms (†1937), Field Museum, *Chicago*; Dr. C. Christensen, Universitetets Botaniske Museum, *Copenhagen*; Sir William Wright Smith, Royal Botanic Garden, *Edinburgh*; Prof. E. Irmscher, Institut für allgemeine Botanik, *Hamburg*; Mr. C. A. Weatherby, Gray Herbarium of *Harvard* University, Cambridge, Mass.; Sir Arthur W. Hill, Royal Botanic Gardens, *Kew*; Dr. W. A. Goddijn and Dr. J. Th. Henrard, Rijks Herbarium, *Leiden*; Miss G. Wigglesworth, *Manchester* Museum; Prof. E. D. Merrill, formerly of the *New York* Botanical Garden; Prof. V. L. Komarov and Dr. V. P. Savicz, the Principal Botanic Garden, *Leningrad*; Prof. B. Fedtschenko and Dr. I. K. Schischkin, Botanical Institute, Academy of Sciences, *Leningrad*; Prof. H. Humbert, Muséum National d'Histoire Naturelle, *Paris*; Mr. G. N. Jones, Washington State Museum, *Seattle*; the Rev. Pater O. Piel, Musée Heude, *Shanghai*; Dr. Harry Smith, Universitetets Botaniska Institution, *Uppsala*; Dr. W. R. Maxon, United States National Herbarium, *Washington*, D.C.; Dr. H. Handel-Mazzetti, Botanisches Institut, Universität, *Vienna*, and Dr. K. Keissler, Naturhistorisches Museum, *Vienna*. I had most of the above collections on loan at the *Cambridge* University Herbarium at the same time; thus it was possible to determine material in many instances by direct reference to type-specimens. Later, thanks to the mediation of Professors H. H. Hu, T. Tang, and F. T. Wang, the Botanical Institute of Sun Yatsen University, *Canton*; the Herbarium of Lingnan University, *Canton*; the Department of Botany of the University of *Nanking*; the Biological Laboratory of the Science Society of China, *Nanking*; and the Fan Memorial Institute of Biology, *Peiping* (Pekin), sent me their material for determination. To the Government Grant Committee of the Royal Society of London I am indebted for grants-in-aid which enabled me to visit the herbarium of the Muséum d'Histoire Naturelle, *Paris*, which possesses Franchet's types, and of Messrs. Vilmorin-Andrieux et Cie at *Verrières-le-Buisson* typifying horticultural names published in *Les Fleurs de pleine Terre*;

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For the abbreviations employed in citing the above herbaria, see p. 444. Plates 26 and 31 and fig. 2 are by Mr. N. K. Gould, figs. 1 and 3–13 by Miss S. Ross-Craig (Mrs. J. R. Sealy), and figs. 15–19 by Mr. A. J. Wise.

HISTORICAL INTRODUCTION.

The name *Ἐπιμήδιον* ('Επιμήδιον) dates from the Greek herbalist Pedanios Dioscorides of Anazarba and his Roman contemporary Pliny the Elder; but it is evident from their descriptions * and from a figure in the 'Codex Aniciae Julianae, nunc Vindobonensis' (6th cent. A.D. copy of an earlier MS. ; original at Vienna, facsimile published in 1906 at Leiden), that their plant, whatever it may be, is not the European barrenwort (*Epimedium alpinum* Linn.) with which sixteenth century herbalists identified it. The latter plant, a native of south Europe, found its way between 1558 and 1597 into gardens of the curious in England and abroad. It was cultivated at Uppsala and in Clifford's garden at Hartecamp, Holland, during Linnaeus's connexion with

* Dioscorides (Mat. Med., lib. iv, cap. 19 : 1st cent. A.D.) describes ἐπιμήδιον as having a stem of no great size, ten or twelve ivy-like leaves, and a slender black root of strong smell but insipid taste; it grew in watery places, formed neither flower nor seed; its special virtue (to quote from Parkinson's translation, of the year 1640) was 'to keepe womens breasts from growing over great being made into a cataplisme, with oyle and applied thereto : . . . the roote would make women barren [whence Gerard's name ' Barrenwort '] that tooke it inwardly, as also the leaves made into powther and taken in Wine '. Pliny (Hist. nat., lib. xxvii, cap. 53 ; 1st cent. A.D.) adds that it had the property of thickening and cooling and was to be avoided by women. Colonna identified the plant with *Botrychium Lunaria* Linn.; C. Bauhin with *Ornithogalum narbonense* Linn.; while both Valerius Cordus and Caesalpino applied the name to *Anemone Hepatica* Linn. (*Hepatica nobilis* Mill.) and Thalius to *Caltha palustris* Linn. Most herbalists, however, took it to be the plant now called *Epimedium alpinum*, although the rhizome of this has a faint smell and a bitter taste. The young plant figured as Ἐπιμήδιον in the 'Codex Vindobonensis', 105 verso (reproduced in Goodyer, Greek Herbal, ed. Gunther, 417) belongs to none of these ; its alternate, distinctly petioled, cordate, and deeply tri-lobed leaves resemble those of several other plants as figured in this MS.—'Αιθίλια more properly Ασκληπιάς (C. V. fol. 47 verso ; Goodyer, 337), 'Απόκυννον (C. V. fol. 68 verso ; Goodyer, 479), "Ερίνος more properly 'Ελξίνη (C. V. fol. 106 verso ; Goodyer, 433), Κιτσός (C. V. fol. 174 verso ; Goodyer, 226), Σμιλλαξ λεία (C. V. fol. 332 verso ; Goodyer, 536)—but it cannot be definitely identified with any of them.

The etymology of the name is obscure : the usually accepted derivation—' from *epi*, upon, akin to, and *Medion*, a plant, said to grow in Media' (Nicholson, Ill. Dict. Gard. I, 515 ; Wittstein, Etym.-bot. Handwör., p. 326)—is hardly convincing. In some texts of Pliny *Epimenidium* occurs instead of *Epimedium* and the earliest surviving Greek herbal, Theophrastos's 'Enquiry into plants', lib. vii, cap. 12 (Loeb Library, transl. by Hort), mentions α σκίλλα ή Ἐπιμενίδειος, i.e. an 'Epimenides squill, which gets its name from its use'. Accordingly it seems possible that *Epimedium* may be a contraction of an earlier name connected with the poet and prophet Epimenides (6th cent. B.C.), of Cnossos in Crete, who apparently dabbled in magic ; the Greeks had a number of plant names, e.g. *Artemisia*, *Achilleios*, *Daphne*, *Gentiane*, *Paonia*, *Telephon*, *Teukrion*, *Hyakinthos*, etc., derived from personal names.

these gardens, and, being the only *Epimedium* known to him, is the type of the generic name as used nowadays. The genus was defined first by de Tournefort, in French in 1694, and in Latin in 1700 :—‘ *Epimedium est plantæ genus, flore cruciformi, quatuor scilicet petalis tubulatis constante. Ex cuius calyce surgit pistillum, quod deinde abit in fructum seu siliquam unicapsularem, bivalvem, et seminibus foetam.* *Epimedii* species unica hactenus cognita. *Epimedium* Dod. Pempt. 599. *Epimedium quorundam* J.B. 2, 395’ (Inst. Rei Herb., p. 232). Even to-day this definition diagnoses the group if *Aceranthus* be excluded. Tournefort placed *Epimedium* among his herbs with cruciform flowers and one-chambered pistils next to *Chelidonium*, the same characters putting it into the *Tetrandria Monogynia* of Linnaeus ; Adanson (1763) and A. L. de Jussieu (1789) were the first to associate *Epimedium* with *Berberis* and *Leontice*. In 1703 de Tournefort indicated the existence of two other species in the Levant, probably *E. pinnatum* β *colchicum*, and *E. pubigerum* (or else two forms of the latter), which he called *Epimedium Orientale, flore ex albo flavescente* and *E. Orientale, flore albo* (Corollarium, p. 17). Of these no specimens exist in his herbarium at Paris and, as Linnaeus knew only the European *E. alpinum*, to which in 1784 his pupil Thunberg erroneously referred a poor specimen of a Japanese species (probably *E. grandiflorum*), the genus remained more or less monotypic until 1821. In that year Augustin Pyramus de Candolle published *E. alpinum* var. *pubigerum* from specimens collected by Olivier and Brugiére near Istanbul (Constantinople) and *E. pinnatum* from information supplied by F. E. L. Fischer of Moscow, who had found a specimen in Pallas’s herbarium collected by Carl Ludwig Hablitzl * in north Persia. A few years later the introductions of von Siebold attracted attention to the rich flora of Japan. Among a consignment of plants which flowered in the Ghent Botanic Garden there were several Epimedums, and their beauty and interest led Charles Morren and Joseph Decaisne to publish in 1834 the first monograph of the group (Ann. Sci. Nat., 2me sér., Bot. II, pp. 347–61).

Morren and Decaisne recognized six species of *Epimedium* proper, namely *E. alpinum* Linn., *E. pubigerum* (raised from varietal status), *E. elatum*, collected by Jacquemont in India, and three, *E. macranthum*, *E. violaceum*, and *E. Musschianum*, introduced by von Siebold from Japan. At the same time they created a new genus, *Aceranthus*, for a spurless Japanese species, *E. diphyllum*, previously figured by Loddiges, and another new genus, *Vancouveria*, for Hooker’s trimerous-flowered *E. hexandrum*, which Menzies, Scouler, and Douglas had collected in North America ‡. The genus was thus shown to occur in Europe and eastern and western Asia, with a close ally in America. Cosson’s discovery of *E. Perralderianum* in 1861 extended its

* Carl Ludwig Hablitzl (1757–1821), a student of S. G. Gmelin and a friend of Pallas, collected in Gilan in 1773 ; see S. G. Gmelin’s ‘ Reise ’, IV, pp. 132–218 (1784).

† In 1837 Rafinesque (Fl. Tellur., nos. 187–9, p. 636) independently took the same view, founding a new genus (*Vindicta*) on *E. diphyllum* and another (*Sculeria*) on *E. hexandrum* ; his third genus (*Endoplectris*) he based on *E. grandiflorum*.

area to north Africa. Of the rich *Epimedium* flora of west and central China * little was known until Maximowicz in 1877 described *E. pubescens* from Shensi province, and Franchet, working out the collections of the French missionaries David and Perny, described *E. Davidi* and *E. acuminatum* from Szechwan and Kweichow provinces. Two important papers belong to this period. Since the introduction of the large-flowered *E. grandiflorum* (*E. macranthum*) the genus had received much attention from cultivators, and, while many new forms had been described and figured, in gardens and nurseries the plants had become greatly confused as to names. This chaos induced J. G. Baker to publish in the 'Gardeners' Chronicle' for 1880 a synopsis of the cultivated forms and species at Kew. Baker's work was overlooked by Franchet, who a few years later (1886) published his paper 'Sur les espèces du genre *Epimedium*' (Bull. Soc. Bot. France, xxxiii, pp. 38-41, 103-16), in which another attempt at reducing the cultivated plants to order and giving an account of the wild species was made. Following Baillon, Franchet referred both *Aceranthus* and *Vancouveria* back to *Epimedium*, and proposed a new sectional classification based primarily upon the disposition and number, or the lack, of leaves on the flowering stem. After uniting *E. macranthum* and *E. violaceum* he recognized eleven wild species. With the cultivated plants he was less at ease, but enumerated them alphabetically at the end of his paper with suggestions as to their possible affinities. Under *E. (Vancouveria) hexandrum* he confused the true *E. hexandrum* of Hooker and another species which was carefully distinguished from it in the next year (1887) by Silvio Calloni as *Vancouveria planipetala* and later (1890) by E. L. Greene as *V. parviflora*. Greene had already (1885) described *V. chrysantha*, and thus within a few years the three American species became known. This paper by Franchet is the classic account of *Epimedium*.

Another revision appeared in 1908 as part of V. L. Komarov's 'Prolegomena ad floras Chinae necnon Mongoliae' (Acta Hort. Petrop. xxix, pp. 125-51, 366-8). Komarov studied *Epimedium* primarily for its interesting distribution, and the detailed systematic part of his work is unsatisfactory, although accompanied

* Native Chinese literature on *Epimedium* is meagre. The name 'Ying yang huo' (cf. p. 508 forward), traditionally applied by Chinese druggists to the dried leaves of *E. sagittatum* and *E. grandiflorum*, occurs in the Emperor Shen-nung's *materia medica*, *Pen ts'ao ching* (between B.C. 202 and A.D. 221), and again in the *Ming i pie lu* (between A.D. 221 and 536); but the sixteenth century encyclopaedist Li Shi-chen in his *Pen ts'ao kang mu* seems the first to describe an *Epimedium* (i.e. *E. sagittatum*) recognizably. For centuries Japanese pharmaceutical works were copies or adaptations of the Chinese, and the first original Japanese works referring to *Epimedium* belong to the eighteenth century (fide Nakai in litt.) :—Ryoan Terajima, *Wakan sansai dzue*, xci (1712); Ihei Ito, *Koeki chikin sho*, xiii, fol. 7 (1719); Shimada alias Yonan, *Kwa-wi*, iv (*Kusa*), fol. 4 (1765), this recording the colour variants of *E. grandiflorum*. The two celebrated nineteenth century iconographies, the *Honzo dzufu* (or *Phonzo zoushou*), vi, fol. 9-12 (1829), by Tsunemasa Iwasaki and the *Somoku dzusetsu* (or *So mokou zoussetsu*), ii, fol. 44-46 (1856), by Yokusai Iinuma, portray several *Epimedums*.

by suggestive remarks on the distribution and phylogeny of the sections. He admits sixteen species of *Epimedium* and three of *Vancouveria*: for his new species *E. elongatum* (actually from western China) no type, collector, or locality is recorded. Since 1908 eleven more species of *Epimedium* have been described from Asia. *E. Cavaleriei* H. Lév. is *Stauntonia Cavaleriana* Gagnep. (Lardizabalaceae); *E. Komarovii* H. Lév. seems conspecific with *E. acuminatum* Franch.; *E. koreanum* Nakai with *E. grandiflorum* C. Morr.; *E. rotundatum* Hao with *E. brevicornu* Maxim.; *E. Sieboldianum* G. Koidz. was described as Japanese, but the type is a mis-labelled specimen of *E. pinatum* Fisch., a Caucasian species; *E. hunanense* (Hand.-Mazz.) Hand.-Mazz., *E. leptorrhizum* Stearn, *E. membranaceum* K. Mey., and *E. platypetalum* K. Mey. seem valid species: *E. sempervirens* Nakai and *E. setosum* G. Koidz. are provisionally recognized in this account, no material being available: *E. macrosepalum* Stearn is new. Of the six 'new species' of *Vancouveria* described by Greene in 1914 none, in my opinion, is specifically distinct from the three already known.

MORPHOLOGY.

Epimedium (*sensu lato*) is a group of perennial woodland herbs—more often hemicyclopediae than geophytes—spreading vegetatively by woody, irregularly branched, interlacing rhizomes, which creep horizontally a little below the surface with their numerous, fine, moderately branched roots occupying the upper 10–30 cm. of soil.

The rhizome is in general cylindric or slightly nodose and covered with brown membranous bracts, these being comparable to ligulate stipules with the petiole reduced to a minute prominence; the tip turns upward each year, elongating into a leafy aerial shoot which perishes usually before the next season, and growth is continued from buds arising at irregular intervals in bract-axils behind the tip. The form of the rhizome, i.e. the degree of elongation and thickness and also the average size of the terminal winter-bud, is fairly constant for each species, and sometimes offers contrasts of taxonomic value (cf. *E. alpinum* and *E. pubigerum*, pp. 459, 478 forward). It is almost thread-like in certain Chinese species, e.g. *E. sutchuenense*, *E. leptorrhizum*, and *E. platypetalum*, although stouter and more compact in others, e.g. *E. sagittatum*, and may be more than 1 cm. thick in *E. pubigerum* of Europe and Asia Minor. Despite Himmelbaur's suggestion (1913, p. 743) that slender rhizomes characterize the extremes of the generic area and stouter rhizomes the centre, there is no correlation between the form of the rhizome and geographical distribution. The cortex is three or four cells thick. The pericycle frequently contains groups of fibres above the vascular bundles which are unequally sized and spaced and arranged in a loose ring, being separated when young by broad medullary rays; later most, if not all, of the centre and interfascicular space becomes lignified.

The stem is terete and shows little variation. The cortex is two or three

cells thick : inside the pericycle there is a layer of fibres separated, in some species, by parenchyma from the scattered bundles, which are bounded individually on the inside by a fibrous sheath ; they are unequally sized and spaced, tending to alternate as two rings ; chlorophyll occurs in the central and interfascicular parenchyma as well as in the cortex ; the line of demarcation between phloem and xylem is curved inwards. The arrangement of the vascular system is thus of a monocotyledonous type.

The young growths are coiled crosier-like, so that the bend of the stem or petiole emerges first and then draws into the light the downward directed

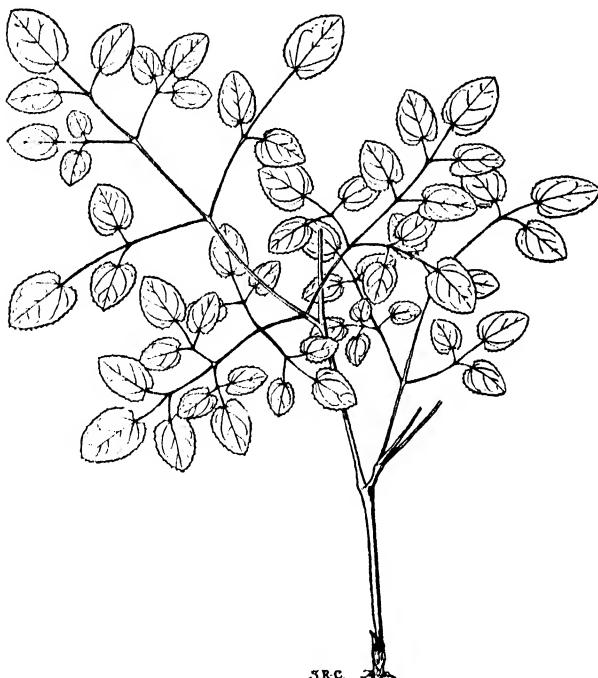


FIG. 1.—Foliage of *Epimedium elatum* from a specimen collected by J. F. Duthie (no. 19133) from the Kagan valley, Hazara, $\times \frac{1}{2}$.

young buds and leaflets ; the latter are involutely rolled and covered with long hairs which usually fall early. The leaves present at flowering time are smaller in length of stalk and area of leaflet than those formed later. The rudiments of the next season's leaves and flower-buds may be found well-formed on dissecting the terminal bud of the rhizome in autumn.

The foliage of *Epimedium* is so characteristic that the group may be recognized by this alone. The compound leaves vary much in degree of subdivision : the leaflets are cordate with slender terete petiolules and are normally in threes. The most widely distributed type of leaf is biennial, occurring throughout the range and in all groups except *Aceranthus* and *Dolichocerae* ; a compound

type seems to be the primitive leaf-form of the Berberidaceae, from which those which are simple have been derived by reduction and fusion. The extreme of leaf-division is found in *E. elatum* (fig. 1); its leaves sometimes consist of more than forty leaflets. The biernate leaf of nine leaflets may be easily modified to an imparipinnate leaf of five leaflets, as in *E. pinnatum* α *originarium*, by the two lateral secondary petioles bearing but one leaflet each, while the median one remains trifoliolate. This imparipinnate type may be further reduced to a trifoliolate type, as in *E. pinnatum* β *colchicum*, *E. platypetalum*, and *E. Davidi* which from the same rhizome produce both three- and five-foliate leaves. Leaves never with more than three leaflets characterize *E. Perralderianum*, *E. pubescens*, *E. acuminatum*, and most species of subsection *Diphyllon*; occasionally these produce basal leaves reduced to only one leaflet. An unusual modification of the trifoliolate leaf is found in *E. diphylum*, the median leaflet being suppressed so that the leaf consists of two very oblique-based leaflets. There is thus a tendency to vary from bi- or even triternate leaves through pinnate to trifoliolate or even bi- or unifoliolate leaves, so that the species of the systematic groups may be arranged in parallel series according to the amount of leaf-reduction.

For diagnostic purposes it is convenient to distinguish leaves arising direct from the rhizome (*folia radicalia*) and those on the flowering stem (*folia caulina*); morphologically they differ little, except that the petiole of a basal leaf broadens at base into a thin ligulate stipular sheath. In *Epimedium* § *Rhizophyllum*, as in *Vancouvereria*, all leaves are basal; in § *Phyllocaulon* the stem bears leaves, although basal leaves are usually present. The actual number of stem-leaves is important: Franchet founded his classification upon it, remarking that it was a feature he had never known to vary in either the wild or cultivated plants. It is not, however, so unvarying as he supposed: in *E. sagittatum* and others, which normally have two apparently opposite stem-leaves, a third leaf sometimes arises at almost the same level as these; while in *Vancouvereria* and in *Epimedium* § *Rhizophyllum* a leaf is occasionally carried up on the flowering stem: such abnormalities do not, however, diminish seriously the practical diagnostic value of the character. There are also plants ($\times E. versicolor$, $\times E. warleyense$), here considered hybrids between *E. pinnatum* (with no stem-leaves) and *E. grandiflorum* or *E. alpinum* (with one stem-leaf), which produce leafless and leafy inflorescences in almost equal numbers from the same rhizome; these plants are known only in gardens. By the normal number of stem-leaves the section *Phyllocaulon* may be divided into three groups:—*Monophyllum* (and *Aceranthus*) having one stem-leaf, *Diphyllon* having two stem-leaves, *Polyphyllum* having several stem-leaves; from the further division of these according to floral characters result quite natural series. In *Diphyllon* the two leaves are usually opposite but occasionally alternate, e.g. in *E. Davidi*; *E. leptorrhizum* is an anomalous species—by the sum of its characters near *E. sutchuenense* (*Diphyllon*, series *Dolichocerae*)—in which the two leaves are unequally developed or one even suppressed, so that in this state it resembles a species of *Monophyllum*; convergence is indicated by

dissimilarity in other characters. Another anomalous species is *E. elongatum*, which usually bears several alternate stem-leaves like *E. elatum* (*Polyphyllon*, series *Elongatae*), but may occasionally have only two opposite stem-leaves as in *Diphyllon*, although its leaflets are different; the position of this species is thus debatable (cf. p. 513). It is significant that the comparatively unstable species occur in western China, where the genus is best represented and where its evolution may still be proceeding.

The *petioles* and *petiolules* are slender, stiff, terete, and have the same general structure as the stem; the scattered bundles often tend to form two rings; the nodes as in *Nandina* are swollen and frequently pilose.

The *leaflets* vary considerably between different species and within a species. They are normally in threes, of which the middle one alone is symmetric; the lateral leaflets have their outer basal lobe larger than the inner lobe, and the outer 'half' of the leaflet is broader than the inner 'half'; this asymmetry is most conspicuous in *E. diphylum* and *E. sagittatum*. The terminal or middle leaflet is somewhat larger than the others. Owing to this variation it is possible to indicate only the general or prevailing form of the leaflets, which may be nearly orbicular, broadly ovate (i.e. length : breadth :: 6 : 5), ovate (length : breadth :: 3 : 2), narrowly ovate (length : breadth :: 2 : 1), or lanceolate (length : breadth :: 3 : 1) according to the species, the broadest part being below the middle; obovate leaflets are unusual. The base is nearly always cordate, with a sinus formed by the two lobes, which may be rounded and overlap behind or diverge at a wide or narrow angle; in *E. sagittatum* the larger lobe is acute or acuminate. The margin is stiffened by a fibrous bundle and usually furnished in *Epimedium* with short spines (up to 2 mm. long in *E. acuminatum* and others), although in *E. diphylum* and *E. pinnatum* β *colchicum* these are often few or even absent: *Vancouveria* always has spineless leaflets. The tip may be mucronate, as in *E. elatum*, or acuminate, as in *E. sutchuenense*, being usually terminated by a spine in *Epimedium* but indented in *Vancouveria*. The young leaflets of *V. hexandra* are peculiar for the hairs they bear on the upper surface, these disappearing with age; in other species of *Vancouveria* and *Epimedium* the upper surface is always glabrous. The cells of the epidermis are irregular in outline, faintly impressing a jigsaw pattern on the cuticle; the stomata, of the usual Ranunculaceous type, occur in the lower epidermis. Like the petioles and flowering stem, the lower leaf-surface is at first covered with long white or reddish hairs usually shed by maturity. They are multicellular, being composed of several superposed more or less equal cells, in most species, but in *E. acuminatum* and *E. sagittatum* there occurs another type of hair with the base formed of several very small cells and the upper part of one or two comparatively long cells. Under a lens, these hairs of *E. acuminatum* and *E. sagittatum* appear as appressed bristles. They are remarkable for developing on old leaves, even after these have acquired their full size; occasionally they are suppressed, so that the leaflet is glabrous. Their development was first studied by Citerne (1892); one of the lower epidermal cells grows into a small conical projection which divides parallel

to the leaf-surface ; the upper half elongates into the long cell, while the lower divides again into three or four basal cells. The lower epidermis is often glaucous ; it may be smooth or papillose, as in certain Chinese species, with rounded projecting cells. The internal structure of the leaf is simple ; there are about four or five layers of rounded cells not very well differentiated into palisade and spongy mesophyll. The primary veins have a fibrous sheath most developed on the lower side and they rise as a network, more or less prominent according to the species, from the surrounding tissue.

The inflorescence may be a simple raceme, e.g. in § *Rhizophyllum*, or a compound raceme having the upper pedicels one-flowered and the lower peduncles cymosely several-flowered, e.g. in *E. acuminatum*, *E. elongatum*, or all peduncles several- (usually 3- or 5-) flowered as in *E. sagittatum*, *V. planipetala*, etc. ; *E. elatum* has a very large loose panicle of branching peduncles. In connexion with Vavilov's law of homologous series in variation, it is of interest to note that the allied species *E. sagittatum* and *E. pubescens* both divide into geographic races or subspecies characterized by compact (*E. sagittatum* α *typicum*, *E. pubescens* α *primarium*) or broad and loose (*E. sagittatum* β *pyramidalis*, *E. pubescens* β *Cavaleriei*) inflorescences. The pedicels and axis may be glabrous or furnished conspicuously or sparsely with multicellular gland-tipped hairs. Their presence seems a feature liable to much fluctuation within a species and is of little taxonomic value, although some species are always glandular and others nearly always glabrous (cf. *Vancouveria*).

Epimedium has a greater range of flower-colour * than other Berberidaceous genera, varying from white (e.g. *E. diphylleum*) and yellow (e.g. *E. pinnatum*) to rose, crimson, and violet (e.g. *E. grandiflorum*) ; in *Vancouveria* the flowers are white, sometimes lavender-tinged, or pale yellow. Usually the colour is constant for a species, but *E. grandiflorum*, *E. acuminatum*, and *E. membranaceum*

* By the courtesy of the Director of the John Innes Horticultural Institution, Dr. Rose Scott-Moncrieff has kindly made a preliminary examination of the flower-pigments of *Epimedium*. She reports that some ivory anthoxanthin (flavone or flavonol), in varying quantity, occurs in the cell-sap of all forms examined ; this is present alone in the pure white $\times E. Youngianum \gamma niveum$. The other sap-pigment is a 3-pentose-glycosidic or 3-monoglycosidic anthocyanin of the delphinidin or petunidin type, this being responsible for the red coloration of *E. alpinum*, $\times E. rubrum$, $\times E. versicolor$ α *versicolor*, and $\times E. warleyense$. Yellow results from the presence of plastid pigment ; no yellow (as distinct from ivory) anthoxanthin has been observed in any form. *E. pinnatum* β *colchicum* and *E. Perralderianum* have much plastid yellow with a trace of ivory anthoxanthin ; $\times E. versicolor$ γ *sulphureum* (*E. pinnatum* $\times E. grandiflorum$), plastid yellow likewise but less than in these species ; *E. alpinum*, much anthocyanin in its sepals, associated with anthoxanthin and a trace of plastid yellow, and no anthocyanin but much anthoxanthin and a trace of plastid yellow in its petals ; $\times E. rubrum$ (*E. alpinum* $\times E. grandiflorum$), less anthocyanin and less anthoxanthin than *E. alpinum* in its sepals and less anthoxanthin but a trace of anthocyanin in its petals ; $\times E. Youngianum \gamma niveum$, much ivory anthoxanthin, but no anthocyanin, and no plastid yellow ; $\times E. Youngianum \beta roseum$, anthoxanthin, with a little anthocyanin but no plastid yellow ; $\times E. warleyense$ (*E. pinnatum* $\times E. alpinum$), anthocyanin, plastid yellow in greater quantity than in *E. alpinum* and much ivory anthoxanthin. These results, though necessarily provisional owing to limited material, support the view that the cultivated forms described on pp. 158-525 are hybrids.

are heterochromic. The flowers are of frail texture and soon fall. They are protogynous and visited by bees for the nectar concealed within the usually saccate or spurred petals. Loew observed *Osmia rufa* visiting cultivated *E. pinnatum* (probably β *colchicum*) and *Bombus agrorum* visiting \times *E. rubrum*; Knuth describes the honey-bee (*Apis mellifica*) as methodically sucking the nectaries of *E. alpinum* and touching and dusting the stigma with pollen brought from another plant; I have watched it at work on *E. pinnatum* β *colchicum*.

The flowers of *Epimedium* and *Vancouvereria* are regular and gamophylloous. Surrounding the androecium and gynoecium are three false-whorls of floral segments, for which various terms have been used in systematic literature. In this paper the outer segments are called 'outer sepals' or 'sepala exteriora' ('sepala' Morren and Decaisne; or 'bracteae' Franchet); the middle segments 'inner sepals' or 'sepala interiora' ('petala' Morren and Decaisne; 'sepala' of Franchet); the inner segments 'petals' or 'petala' ('nectaria' of Morren and Decaisne; 'petala' of Franchet). Komarov makes the consultation of his work difficult by using three sets of terms indiscriminately, the outer sepals being called 'bracteae' in some descriptions, in others 'sepala exteriora' or 'sepala'; the inner sepals 'sepala', 'sepala interiora' or 'petala'; the petals 'petala' or 'nectaria', so that the 'petals' of one description correspond to the 'sepals' of another or the 'petals' of one to the 'nectaries' of another, which is a little confusing. The segments of one false-whorl are opposite those of the next, this arrangement resulting from the compression of two whorls into one false-whorl. The aestivation is imbricate.

In *Epimedium* (a dimerous group) two pairs of small membranous scales or 'outer sepals' compose the outer false-whorl; there may also be two additional, usually deltoid, bracts appressed to the outside of the bud. In *Vancouvereria* there are six to nine outer sepals. These fall as the flower opens and so have little diagnostic utility: nevertheless, their form when mature is fairly constant and distinctive. The inner are larger than the outer. They are frequently narrowly ovate, but may be broadly obovate or oblong, blunt or subacute, from 1-5 mm. long, 1-2 mm. broad, according to the species. In *Vancouvereria hexandra* and *V. chrysanthra* they are beset with very short glandular hairs, but they are glabrous in *V. planipetala* and nearly all species of *Epimedium*.

The two inner false-whorls form the conspicuous part of the flower and exhibit great variation in size and shape. In *Epimedium* there are normally four segments to a false-whorl, but in *Vancouvereria* six, this being characteristic of most Berberidaceae. *E. diphylum* approximates most to the general type of the family; its inner sepals are narrowly ovate, about 6 mm. long, 3 mm. broad, and almost as large as the obovate spurless petals. The relation in size between the petals and inner sepals is important. In the section *Rhizophyllum* (*E. pinnatum* and *E. Perralderianum*), where the petals are reduced to small nectariferous sacs, the yellow, broadly ovate, elliptic or obovate, rounded inner sepals are large and conspicuous. The inner sepals also much exceed the petals in the group *Diphyllon*, series *Brachycerae*, unless, as in *E. sagit-*

tatum, both alike have been greatly reduced. Remarkably long, acuminate, narrowly ovate inner sepals, about 1·7 cm. long, 3 mm. broad, occur in *E. Fargesii* and *E. sutchuenense*. Other distinct kinds are the narrowly ovate, dorsally concave, and boat-like inner sepals of *Monophyllum*, series *Microcerae* (*E. alpinum* and *E. pubigerum*), the obovate clawed inner sepals of *Vancouvereria*, and the minute triangular inner sepals of *E. platypetalum*. At anthesis they spread widely or even reflex, e.g. in *E. Fargesii* and *Vancouvereria*.

The six (*Vancouvereria*) or four (*Epimedium*) segments constituting the innermost false-whorl, the nectaries of some authors, are here called *petals*; as Citerne remarks, there is no reason to consider them as nectariferous glands become petaloid or as staminodes; they are true petals with nectariferous tissue on their inner face. Their form and size are of great taxonomic importance. In *E. diphylum* and *E. platypetalum*, the species which constitute subsection *Aceranthus*, they are obovate, rounded at the tip, and more or less flat with a slight median nectariferous furrow. *Vancouvereria planipetala* also has flat petals, but they are minute and of quite different shape, having the tip divided into three deltoid lobes of which the outer are nectariferous. In *V. hexandra* and *V. chrysantha* the petal consists of a narrowly oblong or cultrate stalk expanded and bent over at the tip so as to enclose the nectariferous tissue in a pocket. In other species of *Epimedium* the petal bulges outwards above or at the base as a blunt nectariferous sac or an acute spur (*calcar*), the form and size being characteristic of the species. The area of nectariferous tissue bears no relation to the length of the spur and is confined to the inside of the tip. It consists of several layers of close small many-sided cells supplied by a vein running straight from the base of the petal, the lateral veins not reaching so far, and covered by an epidermis of more cubical cells with a thin cuticle through which the liquid nectar diffuses into the cavity of the petal.

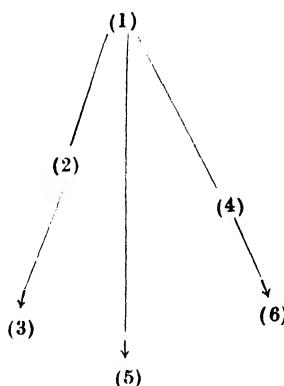
Accepting the flat petal of *Aceranthus* as nearest to the ancestral type, one can imagine the development of the other petal-types from this by the protrusion outwards of the basal portion to form a pouch, small and blunt in some species, elongated and tapering in others, with nectariferous tissue on the inside of the tip, this process being sometimes accompanied by the reduction of the flat petal proper (*lamina*) to a mere fringe around the mouth of the cavity. Thus one can distinguish six main types in *Epimedium* :—

- (1) Lamina flat, obovate, with a slight median nectariferous furrow but no spur, e.g. *E. diphylum* and *E. platypetalum*.
- (2) Lamina rounded and conspicuous, but expanded outwards at base into an elongated spur usually longer than the inner sepal, e.g. *E. grandiflorum*, *E. Davidi*, and *E. hunanense*.
- (3) Lamina reduced to a rim around the mouth of the elongated basally-swollen spur which is longer than the inner sepal, e.g. *E. acuminatum*, *E. membranaceum*, and *E. elongatum*.
- (4) Lamina reduced to a rim around the mouth of the slipper-like cylindric

spur, which is shorter than the inner sepal, e.g. *E. alpinum*, *E. pubigerum*, *E. Fargesii*, and *E. elatum*.

(5) Lamina reduced to a lacerated quadrate fringe at the mouth of the minute spur, e.g. *E. pinnatum* and *E. Perralderianum*.

(6) Lamina and spur alike reduced, forming a minute pouch, e.g. *E. sagittatum* and *E. pubescens*.



A classification based entirely on the form and size of the petal is thus fairly natural, but sometimes brings together plants of different taxonomic groups, indicating probable parallel development. The stages by which these types may have been formed is indicated in the annexed diagram. The same process of petal reduction has apparently taken place within *Leontice* (sensu lato, Prantl), the petals being large and flat (cf. no. 1) in *Bongardia*, much smaller in *Gymnospermium*, and represented by scale-like nectaries (cf. no. 6) in *Caulophyllum* and *Leontice* (sensu stricto = *Euleontice* Prantl).

The stamens are four in *Epimedium*, six in *Vancouveria*, and are opposite the perianth segments. They stand erect, connivent, and more or less appressed to the ovary, and are usually about 5 mm. long; *E. Fargesii* with stamens up to 10 mm. long is a striking exception. They protrude in some species, but are enclosed by the petals in others. The filament varies in length from species to species, being extremely short with the anther almost sessile as in *E. diphylum*, about as long as the anther is in *E. pinnatum*, and many times longer than the anther in *E. Fargesii*. The relation of anther to filament is constant and supplies specific characters. In *Epimedium*, and in *Vancouveria planipetala*, the stamens are glabrous, but in *V. hexandra* and *V. chrysanthra* they are dotted with very short glandular hairs. The anther is basifixied, as in other Berberidaceae, with two pairs of pollen-sacs and opens outwards by two oblong valves which separate from the anther along their base and sides, but remain attached at the top, curling up and crowning the stamen. The pollen is usually yellow, but is green in *×E. warleyense* and *E. pinnatum* γ *circinatum*; the grains are elliptic, smooth (psilate), with three longitudinal furrows.

The normal *gynoecium* is usually regarded as consisting of a single carpel* with parietal placentation, the several horizontal or slightly ascending ovules being in two close rows ; Marchand in 1864, however, described an abnormal plant, cultivated at Paris as '*E. Muschianum*', which had up to nine, mostly aborted, carpels, and also produced a bilocular ovary with axile placentation ; the latter probably resulted from the juxtaposition and fusion of two perfect carpels along their ventral suture. The ovary is externally glabrous in all the species examined, except *Vancouveria hexandra* and *V. chrysanthra*, although described as ' minute puberulo ' in *E. setosum* by Koidzumi (1932). A curved almost longitudinal furrow marks it into two unequal valves ; the larger (adaxial or ventral) bears the style and ovules, the smaller (abaxial or dorsal) is sterile. Each has its own system of venation with a mid-rib (composed of several bundles in the adaxial valve, of one in the abaxial) passing from base to tip and giving off on each side a number of short curved or irregularly bent, simple or forked veins (fig. 2). The adaxial system is more developed than the abaxial. The two systems do not fuse or interlock, and it is along the comparatively weak unveined band of tissue, scarcely 1 mm. broad, lying between them that the *fruit* (which is a thin-walled capsule like the original carpel in form but larger) splits into two valves. The larger valve bears the seed or seeds and the persistent somewhat elongated style. When nearly mature the capsule has some diagnostic value ; it is short and ovoid in many species, but cylindric and more elongated, up to 2·5 cm. long, in others. The *style* is usually shorter than the ovary ; it attains 4·5 mm. in *E. Fargesii* ; the *stigma* is slightly dilated and hollowed out above. The *seeds* are small, about 3-4 mm. long, and weighing about 0·007 gramme in *Vancouveria* (*V. planipetala*) and 0·003-0·004 gramme in *Epimedium* (*E. pubigerum*, *E. acuminatum*), with a smooth chestnut-brown to almost black testa and

* The interpretation of the gynoecium in *Epimedium* and other Berberidaceae presents difficulty. In 1834 Morren and Decaisne described it as formed of two leaves ('deux folioles opposées'), a view revived and ingeniously elaborated by Edith R. Saunders (1925 ; see also Saunders, *Floral Morph.*, 40, 1937). Accepting the *Epimedium* gynoecium as formed of two carpels that are unequal but not fundamentally distinct (i.e. not 'valve' and 'semi-solid'), Marjorie Chapman (1936) postulates for the family Berberidaceae an ancestral type with three spirally arranged free carpels, the upper one of which in *Epimedium*, *Vancouveria*, etc., is presumed to have been lost in the process of fusion, the middle one contracted, and the lower one laterally expanded, thus forming the present normally one-chambered ovary. On the other hand, Theo Eckardt ('Untersuch. Morph. pseudo-monomeren Gynoeciums', *Nova Acta Leopoldina*, N.F., v. no. 26, pp. 1-112, esp. 95-99; 1937), while finding 'pseudomonomery' of the gynoecium evident in *Ulmaceae*, *Moraceae*, *Urticaceae*, etc., does not accept the Berberidaceous gynoecium (e.g. of *Nandina*, *Podophyllum*, *Jeffersonia*) as formed of more than one carpel, since the double system of veining, on which this view is largely based, appears to be foreshadowed in the veining of monomerous carpels of *Ranunculaceae*. The evidence favours neither view exclusively. It seems best to treat the question of whether the *Epimedium* gynoecium is bi- or mono-carpellary as still open.

The embryology of *Epimedium* and other Berberidaceae is described by Johan Mauritzon in *Acta Horti Gotoburg.*, xi, pp. 1-18 (1936).

a thin but conspicuous white unlacerated aril attached around the hilum, which is spongy when fresh and then probably attractive to ants. The seeds of *Epimedium* are nearly sausage-shaped, those of *Vancouveria* semi-orbicular in lateral outline. Citerne noted that the seed-coat becomes disorganized into fibrils when soaked in water. I have observed this in *Epimedium*, but not in *Vancouveria*. The embryo is extremely small, the abundant albumen forming the greater part of the seed.



FIG. 2.—Capsule of *Epimedium pubigerum* by transmitted light, $\times 7$.

Under cultivation in England, *Epimedium* rarely produces seed; consequently only a few seedlings* (these probably from $\times E. Youngianum$ and $E. pinnatum \beta colchicum$) have been examined. At germination, the cotyledons come above ground, whereas in *Caulophyllum* (cf. Butters, 1909) they remain permanently in the seed and no aerial growth appears during the first season; the seedlings of *Epimedium* at first resemble those of *Mahonia* and *Berberis*.

* According to Miss A. Baring, who raised these, seed sown in September germinated the following March.

(cf. Citerne, 1892; Lubbock, 1892), and at all stages are very unlike those of *Podophyllum* (cf. Holm, 1899; Lubbock, 1892) and *Glaucidium* (cf. Kumazawa, 1930). The two cotyledons are narrowly oblong, blunt, sessile, glabrous, ± 4 mm. long, 1 mm. broad; the short hypocotyl becomes woody with age. In its first year the seedling may produce up to six unifoliolate leaves, the extremely short epicotyl being hidden by the sheathing bases of their petioles; each leaf has a slender, wiry, slightly hairy petiole, with a stipulate base and a swollen tip, and a deeply cordate, suborbicular, slightly spinous-margined leaflet which is glabrous above but pubescent beneath and from 1.5 cm. (oldest leaf) to 4 cm. (youngest) long and broad. Since more or less rounded cordate leaflets thus characterize both the seedling and the adult

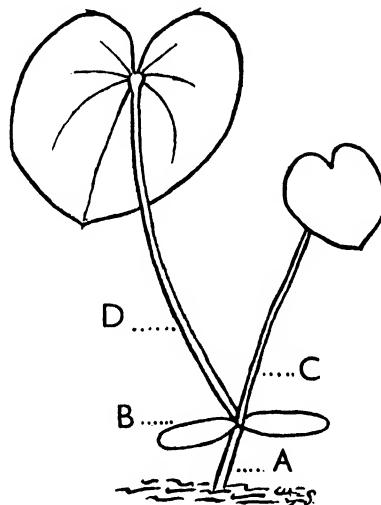


FIG. 2 bis.—A seedling of *Epimedium*, probably *E. pinnatum* β *colchicum*.
a, the hypocotyl; b, cotyledons; c, the first leaf; d, the second leaf.

state of *Epimedium*, but usually only the seedling state of *Mahonia* and *Berberis* (they persist to the adult state in a few species, e.g. *B. agapatensis* Lechler, *B. dolichobotrys* Fedde, *B. hakeoides* (Hook. f.) C. K. Schneider), they give support to the view (Himmelbaur, 1913) that these shrubby genera have evolved from an *Epimedium*-like type. In *Caulophyllum* the epicotyl gradually elongates into a horizontal rhizome, while in *Berberis* and *Mahonia* it becomes the main stem. In *Epimedium* the epicotyl makes no appreciable growth after its first season; instead, buds develop from the axils of the cotyledons and the two lower leaves and form short horizontal rhizomes covered with overlapping bracts; adventitious roots grow down from the axils of these and soon render the plant independent of its tap-root. The leaves on these lateral shoots are tri- or bi-foliolate with hairy petioles and petiolulate leaflets not unlike those of the mature plant. The creeping geophytic habit and other adult characteristics thus early become manifest.

From the other genera of Berberidaceae subfamily Berberidoideae (cf. Engler and Gilg, 1924), *Epimedium* sensu lato * is well defined ; its nearest ally seems to be the monotypic Japanese genus *Ranzania* (*Yatabea*), and, although now a specialized group, it may be nearest in general character to the stock from which *Caulophyllum*, *Gymnospermium*, *Leontice* (a group adapted to xerophytic conditions), and *Achlys* (a very reduced type in every respect), as well as *Berberis* and *Mahonia*, have diverged.

CLASSIFICATION.

The first classification of *Epimedium* was proposed by Morren and Decaisne in 1834, who recognized six species of *Epimedium* proper (i.e. with spurred dimerous flowers) and two monotypic genera, *Aceranthus* and *Vancouveria*, of debatable autonomy. Admitted by Bentham and Hooker, these have been fused with *Epimedium* by all others who have studied the whole group, e.g. by Baillon, Franchet, Prantl, Citerne, Tischler, Komarov, and Himmelbaur. A middle course is adopted here. The type of *Aceranthus*, as also of *Vindicta* Rafin., is *E. diphylum* Lodd., a Japanese species with flat obovate petals and peculiar bifoliolate leaves, the median leaflet of the usual *Epimedium* triad being suppressed. On these characters Bentham maintained the genus, but, as similar ecalcarate petals occur also in a Chinese species (*E. platypetalum*) with three- or five-foliolate leaves of the usual generic pattern, and as there exist plants (cf. $\times E.$ *Youngianum*=*Bonstedtia* Wehrh.) which produce spurred and spurless flowers in the same raceme and are intermediate in leaf-habit between *E. diphylum* and *E. grandiflorum*, the maintenance of *Aceranthus* as a genus is artificial and impracticable.

For *Vancouveria* there is a better case, as it is an American group with flower-parts in threes ; the Old-World Epimedums have flower-parts in pairs. The three species form a homogeneous natural group, recognizable at a glance by their rhizomes, spineless and often trilobed leaflets, scapes of small trimerous flowers, reflexing † obovate inner sepals, and clawed petals, as well as by their semiorbicular seeds. Their facies is thus distinct from that of the Old-World Epimedums, among which nearly all these characters occur individually. Both groups have six pairs of chromosomes (Langlet, 1928 ; Miyaji, 1930). The number of flower-parts, the form of the seeds (to a certain extent), and the geographical distribution furnish the only constant distinctions, and it is accordingly a matter of taste whether they should be treated as genera or subgenera. They are certainly 'natural genera' in the sense of being 'genera with a tolerably uniform facies as well as floral structure and at the same time a range suggestive of a continuous common history of their members' ‡ and, since *Vancouveria* has been used in all American floras and most horticultural

* For figures and descriptions of this curious plant, see Yatabe, Icon. Fl. Jap. I, t. 22 (1892) ; Tischler in Engl. Bot. Jahrb., XXXI, pp. 677-79 (1902) ; [Higgins & Stearn in] Quart. Bull. Alp. Gard. Soc., V, pp. 223, 226 (1937) ; Kumazawa in Jap. Journ. Bot., IX, pp. 55-70 (1937).

† Whence the American popular name 'Inside-out flower'.

‡ Cf. Stapf in Bot. Mag., under t. 8985.

works since 1834, it seems best to follow the traditional treatment on grounds of convenience.

The six remaining species were placed by Morren and Decaisne in two sections, the large-flowered Japanese species (*E. grandiflorum* and forms) in their section *Macroceras*, the others (*E. alpinum*, *E. pubigerum*, and *E. elatum*) with smaller flowers and blunt spurs in their section *Microceras*; this is a fairly good arrangement when confined to these, but becomes inadequate and artificial if extended to the many other species now known. The following note of Fischer and Meyer (1846) initiated the present system :—

'Genus *Epimedium* commode in sectiones tres, valde naturales, dividi potest.

I. *Macroceras*. Nectaria lamina explanata erecto-conniventia, basi calcarata vel cucullata. Caulis foliosus. Flores albidi vel violacei.—

Species omnes japonicae.

A. *Calcaria elongata*.

1. *E. macranthum* Morren et Decaisne.
2. *E. violaceum* M. et Den.
3. *E. Musschianum* M. et Den.

B. *Calcaria abbreviata cuculliformia*.

4. *E. Youngianum* Fisch. et Mey. *E. Musschianum* *Botanical Magazine* tab. 3745 (non Decaisne). Species nobis nota solum ex iconе citata, sed ab omnibus descriptis speciebus nectarii lamina explanata petaloidea instructis, calcare abbreviato differt; ab *E. Musschiano* Decaisne praeterea distat foliis biternatis.

II. *Microceras*. Nectaria brevia, depressa, cucullata; lamina nulla. Caulis foliosus. Petala sanguinea.—Species europaeae, unica Indiae orientalis.

5. *E. alpinum* Linn.
6. *E. pubigerum* M. et Den.
7. *E. elatum* M. et Den.

III. *Rhizophyllum*. Nectaria brevia, depressa, cucullata; lamina nulla. Folia omnia radicalia. Scapus aphyllus. Petala flava.—Species caucasica.

8. *E. pinnatum* Fisch.'

E. pinnatum, which Morren referred to the section *Microceras*, is here made the type of a new section, differing from the others by its leafless inflorescence. Sixteen years later Baillon proposed a similar arrangement, his section *Dimorphophyllum* (1862) corresponding to Fischer's *Rhizophyllum* (1846) and Franchet's *Gymnocaulon* (1886); he also retained *Microceras* and *Macroceras* as sections, but added *Aceranthus* and, later, *Vancouveria* (1871) as other sections. The next attempt was made by Franchet in 1886. He proposed the subgenera *Euepimedium* and *Vancouveria*, and emphasized a hitherto little-appreciated

character, the number of leaves borne on the flowering stem. Franchet's classification was accepted by Komarov (1908) and is used here with a few modifications.

The species of *Epimedium* are fairly well defined and fall into eight small groups or series (nos. i–viii of the following table) founded on differences in the relative size and form of the inner sepals and petals as well as habit; it is difficult, however, to find characters, not so widespread as to be generic, nor so limited as to be purely specific, by which these groups may be united into larger groups indicative of supposed phylogeny. After the section *Rhizophyllum* has been separated, the most practical character for further division of *Epimedium* is the number of leaves on the flowering stem. *Monophyllum* has one leaf; *Diphyllum* normally two leaves; *Polyphyllum* several leaves: but, as noted in the account of morphology (p. 417), this is liable to some variation. However, it brings together species alike in many other characters and the groups formed are geographically significant.

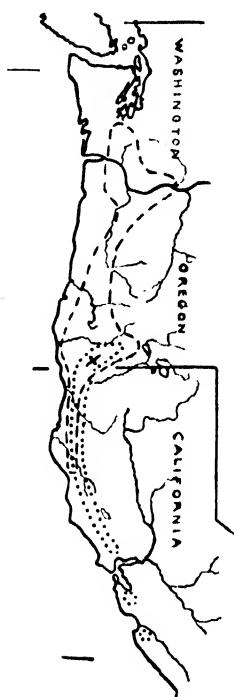
The following is the present system:—

Genus VANCOUVERIA.	$\left\{ \begin{array}{l} 1. V. hexandra. \\ 2. V. chrysantha. \\ 3. V. planipetala. \end{array} \right\}$	Pacific Coast States of North America.
Genus EPIMEDIUM.		
I. Sectio RHILOPHYLLUM (i).	$\left\{ \begin{array}{l} 1. E. pinnatum. \\ 1 \text{ bis. } E. pteroceras. \\ 2. E. Perralderianum. \end{array} \right\}$	Caucasus, north Africa.
		Western or Mediterranean Group
II. Sectio PHYLLOCAULON.		
1. Subsectio <i>Monophyllum</i> .	$\left\{ \begin{array}{l} 3. E. alpinum. \\ 4. E. pubigerum. \end{array} \right\}$	Europe, Asia Minor. Japan, Korea,
Series <i>Microcerae</i> (ii).		Manchuria, Far Eastern Russia.
Series <i>Macrocerae</i> (iii).	$\left\{ \begin{array}{l} 5. E. grandiflorum. \\ 5 \text{ bis. } E. sempervirens. \\ 6. E. macrosepalum. \\ 7. E. diphylum. \\ 8. E. setosum. \\ 9. E. platypetalum. \end{array} \right\}$	
2. Subsectio <i>Aceranthus</i> (iv).		Old World (Northern Hemisphere).
3. Subsectio <i>Diphyllon</i> .	$\left\{ \begin{array}{l} 10. E. Davidi. \\ 11. E. hunanense. \\ 12. E. acuminatum. \\ 13. E. membranaceum. \\ 14. E. sutchuenense. \\ 15. E. leptorrhizum. \\ 16. E. brevicornu. \\ 17. E. Fargesii. \\ 18. E. pubescens. \\ 19. E. sagittatum. \end{array} \right\}$	Eastern or East Asiatic Group.
Series <i>Dolichocerae</i> (v).		China.
Series <i>Brachycerae</i> (vi).		India.
4. Subsectio <i>Polyphyllum</i> .	$\left\{ \begin{array}{l} 20. E. elongatum. \\ 21. E. elatum. \end{array} \right\}$	
Series <i>Elongatae</i> (vii).		
Series <i>Elatae</i> (viii).		

GEOGRAPHICAL DISTRIBUTION.

The present distribution of plants cannot be understood without considering their history and environmental requirements. The requirements of *Epimedium* and its herbaceous allies—*Achlys*, *Jeffersonia*, *Ranzania*, *Caulophyllum*, all woodland plants—are clear, but the fossil record yields no direct information about their former range and wanderings. One can only surmise how their existing range has been attained from what is known of various other groups sharing their habitats and presenting the same peculiarities of distribution.

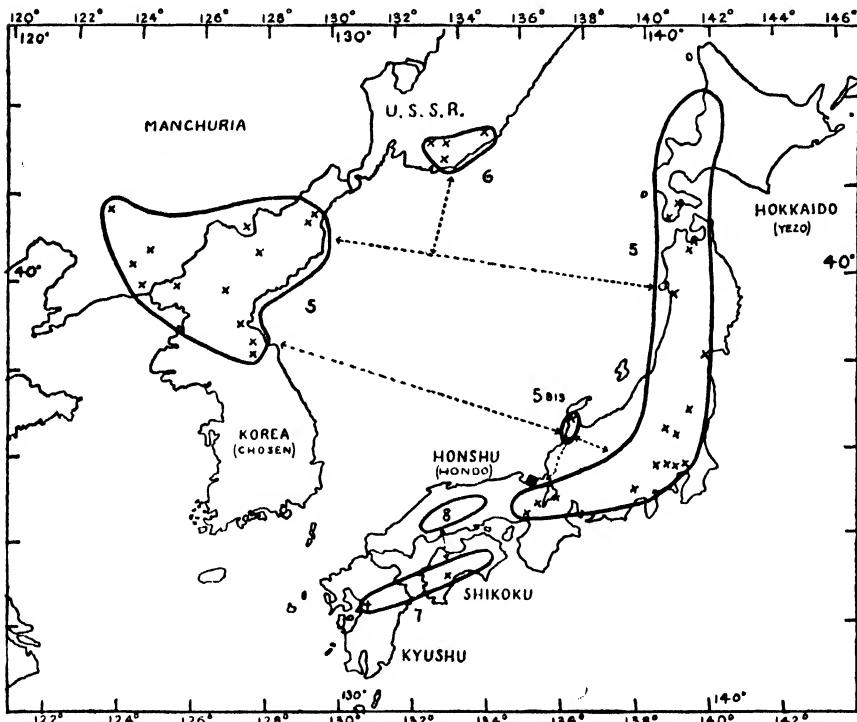
Epimedium proper (§ *Euepimedium* Franch.) is an Old World assemblage. In North America its place is taken by *Vancouveria*, a group of three species



MAP 1.—The distribution of *Vancouveria hexandra* within the boundaries marked - - - and of *V. planipetala* within the boundaries marked *V. chrysanthra* occurs at the mark X.

which extends within the Humid Transition Zone from north Washington to middle California, ranging not more than 130 miles inland; like *Achlys*, an allied Berberid occurring also in eastern Asia, it is absent from Atlantic North America. Essentially woodland plants, the Vancouverias often grow in the shade of redwoods (*Sequoia sempervirens* (Lamb.) Endl.), a suggestive association since, although the two living species of *Sequoia* are confined to California and southern Oregon, the generic range was formerly much greater. *Vancouveria hexandra* (with thin leaflets) is a species found in Washington, Oregon and north California. *V. planipetala* (with coriaceous leaflets) ranges

between middle California and the Rogue River in south Oregon, which marks the northern limit of many Californian plants. Thus their ranges overlap in north California and south Oregon. *V. chrysanthia* (with coriaceous leaflets) is confined to a small area on the Oregon-California boundary within the overlap of its two wide-ranging allies and, though unique in possessing yellow flowers, it otherwise combines their characters. In its trimerous flowers *Vancouveria* furnishes a transition from other Berberidaceae to *Epimedium* proper, and may be regarded as preserving in this respect a primitive

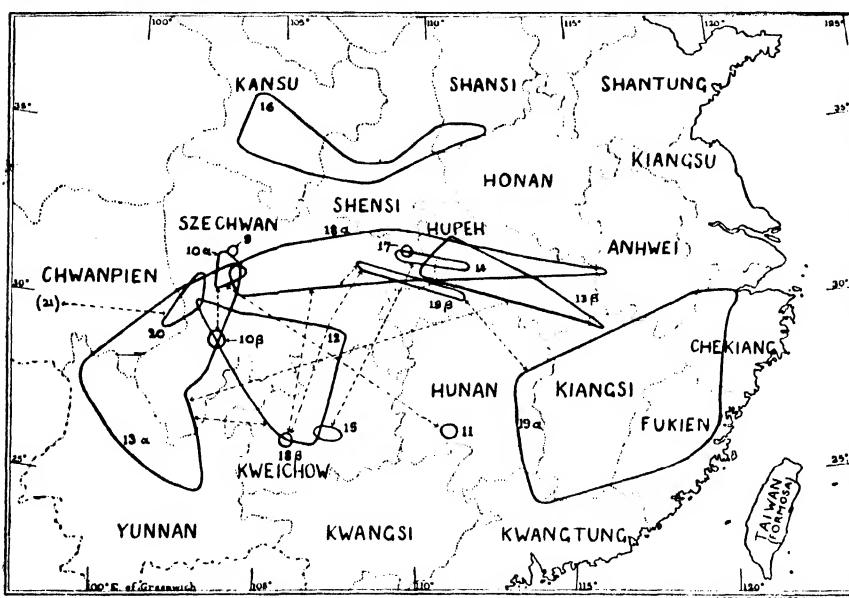


MAP 2.—Distribution of *Epimedium* in Far Eastern Asia. 5, *E. grandiflorum* (incl. *E. koreanicum*) (p. 479); 5 bis, *E. semperflorens* (p. 484); ◊ *E. macranthum* var. *hypoglaucum* (? = *E. semperflorens*) (p. 484); 6, *E. macrosepalum* (p. 485); 7, *E. diphylum* (p. 487); 8, *E. setosum* (p. 489).

condition of the family. In its leafless flowering stems it resembles the Mediterranean *Epimedium* section *Rhizophyllum*.

Epimedium proper occupies two widely separated regions, in east Asia and the Mediterranean lands; within each region there are extensive areas from which the genus is entirely absent; no one species of the genus has a very wide range and many are very local.

The east Asiatic group (cf. p. 428) centres in western China and has outlying members in Kashmir and Japan. Subsection *Monophyllum* (represented also by two species in the Mediterranean region) in east Asia consists of a variable species, *E. grandiflorum*, common to Japan and Korea, and two close allies, *E. sempervirens* apparently endemic to Japan and *E. macrosepalum* to Far Eastern U.S.S.R. (Map 2). Since *Epimedium* is a group confined ecologically to woodland and scrub, and seems able to spread only by the slow process of rhizome growth and the transport of its seeds by ants, this range was most



MAP 3.—Distribution of *Epimedium* in China. 9, *E. platypetalum* (p. 489); 10 α & 10 β , *E. Davidi* α & β (p. 490); 11, *E. hunanense* (p. 492); 12, *E. acuminatum* (p. 493); 13 α , *E. membranaceum* α *genuinum* (p. 495); 13 β , *E. membranaceum* β *orientale* (p. 497); 14, *E. sutchuenense* (p. 498); 15, *E. leptorrhizum* (p. 499); 16, *E. brevicornu* (p. 500); 17, *E. Fargesii* (p. 502); 18 α , *E. pubescens* α *primarium* (p. 503); 18 β , *E. pubescens* β *Cavaleriei* (p. 504); 19 α , *E. sagittatum* α *typicum* (p. 505); 19 β , *E. sagittatum* β *pyramidalis* (p. 508); 20, *E. elongatum* (p. 509); (21), *E. elatum* (p. 511). Arrows and dotted lines connect the more closely related forms.

probably attained before the sinking of south-east Asia had parted Japan from the mainland (i.e. probably during the Pliocene period; cf. Arldt, 1919, p. 422), but, judging from herbarium material, no morphological characters distinguish the long-isolated island from the mainland populations of *E. grandiflorum*. Subsection *Aceranthus*, primitive only in its spurless petals, consists of one or perhaps two species, *E. diphylum* and the doubtfully distinct *E. setosum*, in south Japan and one species, *E. platypetalum*, not at all closely

allied, in western China. Subsection *Diphyllon*, with ten species and their variants—the largest group within the genus—is confined to west and central China. There remains the small subsection *Polyphyllon*, with one species, *E. elatum*, in Kashmir and another, *E. elongatum*, in west China. *E. elatum* is geographically isolated between the east Asiatic and Mediterranean groups and stands morphologically apart from both, though apparently most akin to the east Asiatic group. It is much reduced in floral structure, but, by virtue of its numerous and much divided leaves, suggests a type from which, by reduction, the other leaf-forms of the genus have been derived.

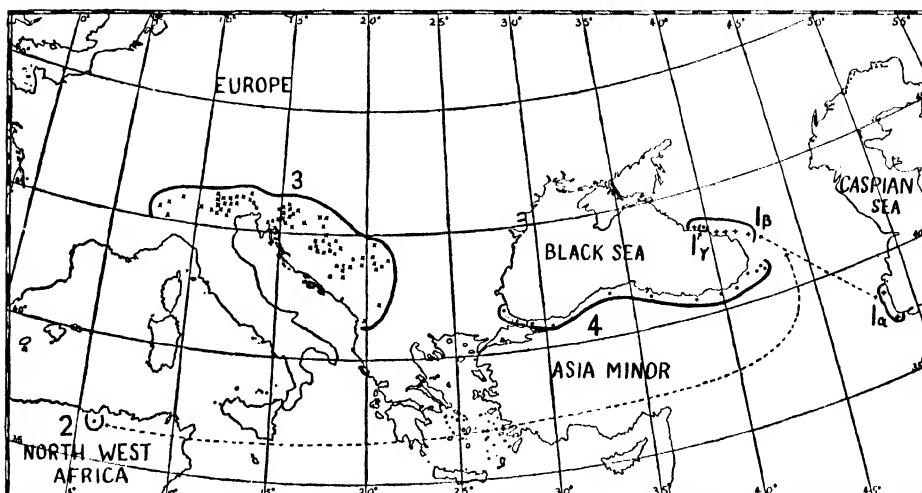
The following list shows the distribution (Map 3), as at present known, of the Chinese Epimediums arranged by provinces; the letter (t) indicates species first described from a particular province, i.e. their type-areas:—

Kansu :—	<i>E. brevicornu</i> (t).	Southern border of North China Loess- Steppe Province.
Shensi :—	<i>E. brevicornu</i> , <i>E. pubescens</i> α <i>primarium</i> (t).	
Shansi :—	<i>E. brevicornu</i> .	
Anhwei :—	<i>E. pubescens</i> α <i>primarium</i> , <i>E. sagittatum</i> .	
Chekiang :—	<i>E. sagittatum</i> .	
Fukien :—	<i>E. sagittatum</i> .	
Hunan :—	<i>E. hunanense</i> (t), <i>E. sagittatum</i> .	
Hupeh :—	<i>E. sagittatum</i> , <i>E. sutchuenense</i> .	
Kiangsi :—	<i>E. membranaceum</i> β <i>orientale</i> (t), <i>E. sagittatum</i> .	
Kwangsi :—	<i>E. sp.</i> indet. (C. H. Chung 8168).	
Kwangtung :—	<i>E. sagittatum</i> , <i>E. sp.</i> indet. (T. K. P'eng 2777).	Middle Sino- Japanese Laurel Province.
Kweichow :—	<i>E. acuminatum</i> (t), <i>E. leptorrhizum</i> (t), <i>E. pubescens</i> β <i>Caerulei</i> (t).	
Szechwan, east :—	<i>E. acuminatum</i> , <i>E. Fargesii</i> (t), <i>E. sagittatum</i> , <i>E. sutchuenense</i> (t).	
Szechwan, west :—	<i>E. Davidi</i> (t), <i>E. elongatum</i> (t), <i>E. membranaceum</i> α <i>genuinum</i> (t), <i>E. platypetalum</i> , <i>E. pubescens</i> α <i>primarium</i> .	
Yunnan :—	<i>E. acuminatum</i> , <i>E. membranaceum</i> α <i>genuinum</i> .	High Mountain Province of Yunnan and West Szechwan.

For biological purposes, however, the eight floral provinces of China (including Korea) proposed by Handel-Mazzetti (1927, 1930, 1931) are more significant than political divisions, and if these be adopted *Epimedium* is found to grow within four of them: (1) the north-east Sino-Korean province of mixed woods; (2) the mountains on the southern boundary of the north China loess-steppe province; (3) the temperate or warm temperate mountain zone to the west of the middle Sino-Japanese laurel province; (4) the temperate or warm temperate zone of the high mountain province of Yunnan and west Szechwan. Thus the genus is absent from tropical China, the desert Gobi, the west Yunnan monsoon province, and the east Tibetan grassland province, and is poorly represented in the northern mixed forest and loess provinces. It avoids cold and dry as well as low, hot, and very moist regions, and grows normally in temperate forest and scrub in mountainous regions. This temperate forest vegetation is now largely restricted to western China, but fossil evidence testifies to its former existence within regions where it no longer occurs or is poorly

represented. The relationship of this former forest extension to the wide and discontinuous range of *Epimedium* will be considered later.

Of the four Mediterranean species (Map 4), two belong to subsection *Monophyllum*: *E. alpinum* (Map 5) is a west Balkan species extending across north Italy along the southern foot-hills of the Alps; its close ally ('espèce jumelle') *E. pubigerum* ranges from the south-east of the Balkan peninsula, in moist woods of *Fagus orientalis* Lipsky, *Populus tremula* Linn., *Prunus Laurocerasus* Linn., *Rhododendron ponticum* Linn., etc., along the northern coastal fringe of Asia Minor to the west Caucasus. Its associates are of interest because fossil remains show them to have been important elements in Tertiary forests. The other two Mediterranean species, *E. pinnatum* and *E. Perralderianum*, make up the section *Rhizophyllum*. They resemble one another



MAP 4.—Distribution of *Epimedium* in the Mediterranean Region and western Asia.—

- 1 α ; *E. pinnatum* α *originarium* (p. 462); 1 β , *E. pinnatum* β *colchicum* (p. 464); 1 γ , *E. pinnatum* γ *circinatum* (p. 466); 2, *E. Perralderianum* (p. 467); 3, *E. alpinum* (p. 470); 4, *E. pubigerum* (p. 476).

closely, but are remarkably distinct from other members of the genus. Two subspecies of *E. pinnatum* (β *colchicum* and γ *circinatum*) inhabit the west Caucasus, while a third (α *originarium*) grows in mountain woods in the east Caucasus and north Persia. Both areas, one by the Black Sea, the other by the Caspian, have a moist temperate climate, approximating to that of the temperate zone of the middle Sino-Japanese laurel province, and are noted for their luxuriant vegetation. The intervening region of the central Caucasus is drier, and *Epimedium*, in common with certain Caucasian genera having Sino-Japanese affinities, e.g. *Pterocarya* and *Zelkova*, is absent from it. The only remaining member of the section *Rhizophyllum*, *E. Perralderianum*,

lives in the mountains of Kabylia in north Africa fully 2,000 miles distant from its nearest allies and is the only African representative of the genus.

Despite the wide and discontinuous distribution outlined above, the ecological requirements of the species appear to be much alike. The frequency of such notes in the literature and on collectors' labels as 'woodland', 'margins of thickets', 'on mossy banks', etc., together with details of altitude and latitude and meteorological data from stations nearest to habitats of *Epimedium*, all point to a prevailing type of habitat for the group as a whole. It seems reasonable to conclude that, wherever *Epimedium* is found, woodland and scrub in temperate hilly or montane regions provide the conditions for its existence and, since the range of species halts abruptly where these ecological and climatic conditions cease, it may well be that without them the genus would not survive.

This ecological uniformity of the genus is confirmed by its behaviour in gardens. Species from Algeria, south Europe, Asia Minor, the Caucasus, and Japan, as well as the Vancouverias from the Pacific Coast of North America, thrive in British gardens under the same cultural conditions, delighting especially in the shelter and dappled shade of light woodland, though able to grow (but less luxuriantly) in sun or on dry banks in shade; nor are they of difficult cultivation elsewhere in north-west and central Europe. Though indigenous only south of the Alps, *E. alpinum* has become naturalized in Belgium, Czechoslovakia, France, Germany, Great Britain, Sweden, and Switzerland. The absence of the genus from north-west Europe to-day cannot be attributed to unsuitable climate; the reason must be sought in past climatic changes.

If the species of *Epimedium* have had a common origin, which there is no cause to doubt, then the generic area cannot always have been so broken. From the ecological and morphological similarity of species now geographically remote, it is reasonable to suppose that their common ancestors had like requirements; in other words, *Epimedium* has always been a group needing the shade of temperate woodland for its survival and spread under natural conditions. If this is accepted, then its wide range at the present day can only be explained by the former existence of temperate woodland in the now treeless or subtropical regions sundering its members.

As a result, primarily, of the work of C. and E. M. Reid (1915; cf. also Reid, E. M., 1920) on the Pliocene flora of north-west Europe, the close resemblance between this and the present mountain forest flora of west China has become almost a palaeobotanic commonplace. As shown by these authors, this resemblance is marked by the presence in Pliocene deposits on the Dutch-Prussian border of 'various species which, although now extinct in Europe, cannot be separated from living Chinese plants', while others have their closest allies in species inhabiting the temperate belt of the Chinese mountains. It is significant that the distribution of *Epimedium* coincides in many respects with the modern distribution of some of these Tertiary genera. Thus *Ptero-*

carya consists of one Caucasian species, one Japanese, and several Chinese : *Zelcova* has to-day one species in the east and west Caucasus and north Persia, with a range very like that of *E. pinnatum*, one in Crete, the others in China. By analogy with these, as also from the existence of herbaceous genera such as *Incarvillea* in Europe during the Oligocene period of the Tertiary era (Bembridge flora), it is reasonable, despite the lack of fossil evidence, to suppose that *Epimedium* had likewise acquired its present form and spread widely long before the end of the Pliocene period. Its marked distinctness from other Berberidaceae suggests that the differentiation of the group must have taken place in a remote period of geological time.

During the early part of the Tertiary, according to Kryshtofovich (1929, 1935), Seward (1931), and other palaeobotanists, an evergreen flora of subtropical aspect flourished in Europe and as far north as west Greenland. In northern Asia there grew summer-green forests built of essentially temperate genera such as *Sequoia*, *Taxodium*, *Fagus*, *Alnus*, *Betula*, *Corylus*, *Juglans*, etc. Their composition was probably not unlike that of the Sino-Japanese mountain forests wherein, as already noted, *Epimedium* is now best represented. This forest-belt is considered to have existed in Asia since the last stages of the Cretaceous. Before the end of the Tertiary a temperate forest flora had spread westward and had become characteristic of Europe. The mild conditions prevailing over the northern hemisphere during most of the Tertiary gave way subsequently to the colder conditions of the Quaternary (Pleistocene or Diluvial) ice-ages. At the periods of maximum glaciation a vast ice-sheet covered Scandinavia, most of Great Britain, and north Germany, while the glaciers of the Alps, the Caucasus, eastern Asia, and elsewhere were greatly increased (cf. Penck, 1906 ; Wright, 1914 ; Antevs, 1929). The Pyrenees, Alps, and Himalaya barred the southward migration of temperate plants retreating from the cold of advancing ice-sheets ; and between the Scandinavian and Alpine ice and north of the Himalaya probably the greater part of Tertiary forest vegetation perished. No such barrier entirely cut off the Balkan peninsula from central Europe ; accordingly it appears to have become an area of refuge and a centre from which, during the long interglacial periods and the postglacial period, the more vigorous types recolonized lost territory ; here *E. alpinum* has its maximum area. Other remnants of temperate Tertiary forest vegetation held out on the southern slopes of the Caucasian and Himalayan ranges ; these are the areas inhabited by *E. pinnatum* and *E. elatum*. The glaciation of western and central Asia was less severe than that of Europe, but the deserts and steppes of these regions do not support forest growth, and *Epimedium* is absent from them. The greatest area of refuge was in western China ; here the mountains trend obliquely north and south, rather than east and west, and upon their high and feebly glaciated slopes plants were able, by climbing or descending as the climate changed from cold glacial to warmer interglacial or vice versa, to keep within the conditions necessary for their survival ; here *Epimedium* reaches its maximum development.

From the facts outlined above *Epimedium* may be regarded as having originated in the north Asiatic forest-belt and shared its history. Such a view would account for the diversity of forms in eastern Asia, where the present mountain forest flora is held to be a lineal descendant of the Tertiary forest-belt. It also accounts for the occurrence of the genus in less abundance in the other regions (Kashmir, Caucasus, Balkan peninsula), where remnants of this forest have survived, and the absence of the genus from regions where—owing to glaciation and other climatic factors—this forest is believed to have suffered destruction or never extended.

The presence in north-west Africa of *E. Perralderianum*, a plant closely related to the Caucasian *E. pinnatum*, can likewise be explained after consideration of former climatic conditions and the ranges of various of its associates.

Between the existing stations of *E. pinnatum* and *E. Perralderianum* stretch over two thousand miles of sea and land, most of the latter being desert and unsuited to the growth of temperate forest vegetation. The area in the mountains of Constantine, Algeria, which *E. Perralderianum* inhabits, is one of the coolest and wettest along the arid north African coast; snow covers it for several months in winter, but little rain falls in summer (Barbey, 1934). Transferred from the mountains to Algiers in the lowlands, *E. Perralderianum* has failed to survive (R. Maire, in litt.); transferred to British gardens the plant waxes to a size unknown under natural conditions. The species is clearly a relict lingering under conditions which approximate sufficiently closely to the usual requirements of the genus for its survival, but apparently not enough for its optimum development.

Of the trees under whose shade *E. Perralderianum* persists upon the Babor Massif, the three most abundant—*Quercus Afares*, *Abies numidica*, *Cedrus atlantica* (cf. Trabut, 1889; Mattfeld, 1925; Barbey, 1934; Elwes and Henry, Trees, iv, p. 738; 1909)—are all likewise noteworthy in being isolated and endemic north-west African species so little differentiated from west Asiatic species as to leave no doubt of their derivation from Asiatic stocks. Thus *Quercus Afares* Pomel is almost conspecific with *Q. castaneifolia* C. A. Meyer, an oak confined, as is *E. pinnatum* α *originarium*, to mountain woods by the Caspian Sea and forming with another Caspian oak, *Q. Sintenisii* O. Schwarz, a distinct group within the genus, the distribution of which (*Quercus* ser. *Castaneifoliae* O. Schwarz) thus parallels significantly the distribution of *Epimedium* section *Rhizophyllum*. Of *Cedrus*, besides *C. atlantica* Manetti, there exist only three species or geographical races, *C. libani* Loudon in Lebanon and Asia Minor, *C. brevifolia* (Hook. f.) Henry in Cyprus, *C. Deodara* (Royle) Loudon in the Himalaya, kept apart by sea and desert areas, but differing little in morphological characters. *Abies numidica* de Lann. is more closely allied to *A. cilicica* (Antoine & Kotschy) Carr., an associate of *Cedrus libani* in Asia Minor, than it is to the geographically nearer *A. Pinsapo* Boiss. of Spain and Morocco. *Populus tremula* Linn., which grows sparsely on the Babor Massif, has here (fide R. Maire) its one station in Africa. These plants can only be regarded

as isolated remnants of a flora which was more widely distributed in Tertiary times. Of this more extensive range, indications have recently been given by Stojanoff and Stefanoff (1929), and by Stefanoff and Jordanoff (1935), in identifying with *Cedrus libani* (*sensu lato*) the fossil cone-scales of a conifer found in Pliocene sediments of the plain of Sofia—for fossil records of *Cedrus* in France, Germany, and Russia during the Tertiary, see Studt, 1926, p. 257—and with *Quercus castaneifolia* (*sensu lato*) the leaf-impressions, fossil cupules, and acorns of the oak formerly distinguished as *Quercus Drymeja* Unger occurring in the same Bulgarian deposits as well as recorded from Austria, Switzerland, Jugoslavia, Italy, Asia Minor, and the Caucasus. The abundant fossil material shows these plants to have been common in the forest vegetation of south-east Europe in late Tertiary times. To-day neither grows wild in Europe. From the same Bulgarian deposits other species found in the Babor forest, i.e. *Populus tremula* Linn., *Ilex Aquifolium* Linn., *Taxus baccata* Linn., and *Acer campestre* Linn., have also been recorded. Possibly these plants reached their present north African habitat by different routes and at different times, but their present restricted association in the Babor forest and their inability to grow in the arid Mediterranean lowlands suggests that they came as a community at a time when the Mediterranean had a higher rainfall and a more temperate climate than it now possesses. In other words, the Babor Massif may be regarded as sheltering a fragment of the Tertiary mixed forest-belt. The clue to its presence in north-west Africa is supplied by the geological evidence brought forward by Blanckenhorn (1910) and Gregory (1911); cf. also Antevs, (1928), as indicating periods of higher rainfall in Syria, Palestine, Egypt, and Cyrenaica in former times. These pluvial periods have been correlated with periods of glaciation in Europe (cf. Brooks, 1922; Woldstedt, 1929) and attributed to the turning southward, by the high pressure areas over the great Scandinavian and Alpine ice-sheets, of the storms from the Atlantic which now water Europe north of the Alps. During such a period a temperate forest-flora could extend westward along the north African coast from Asia. At the close of such a period this flora could only survive by ascending the mountains in the west, the region to which *Cedrus*, *Abies*, *Quercus*, and *Epimedium* are now confined in Africa. With regard to the length of time these north African plants have been cut off from their west Asiatic representatives, it may be mentioned that the deposit by the Nile of the alluvial muds south of Cairo, which is regarded as beginning towards the end of the last glacial period (cf. Brooks, 1922, pp. 72-4), is calculated to have taken about 14,000 years. The isolation of *Cedrus*, *Abies*, *Quercus*, and *Epimedium* probably came about much earlier than this, for no gravel terraces such as indicate pluvial conditions in Egypt during the Günz, Mindel, and Riss glaciations of the Alps are known for the Würm (last glacial) period, and the climate may have been dry and semi-desert from the beginning of the Riss-Würm interglacial (Blanckenhorn, 1910, p. 422), i.e. for about the last 100,000 years (Brooks, 1922, pp. 48, 74). If so, the feeble differences achieved illustrate the slowness of evolutionary change in these groups.

As already noted, the species and subspecies of *Epimedium* are usually both geographic and morphological entities ; in other words, a species of more or less continuous range is fairly homogeneous, but when the range is broken the isolated populations often, but by no means always, differ to an extent sufficient for their recognition as subspecies or species. Floral differences are usually correlated with differences in rhizome, leaf, or inflorescence ; most of the species are well defined and occupy areas separated from those of their nearest allies. Within certain species occur races less well defined, possibly connected by intermediates or differing in only one character, but with geographical significance ; these are here treated as subspecies. A consideration of the differences between these groups (cf. key-contrasts, pp. 458-461) reveals few of such utility and direct survival value as to have been developed through natural selection. In general life-form all are much alike and grow under fairly similar conditions ; the most striking specific differences appear of neutral value in the struggle for existence. Thus the series *Dolichocerae* (*E. acuminatum* and allies) and *Brachycerae* (*E. sagittatum* and allies) are very distinct in flower, but vegetatively some members of the one resemble so closely some members of the other as to be hardly distinguishable out of flower. Both are of comparatively wide distribution in China and occupy similar habitats ; accordingly their differences appear uncorrelated with the environment, and neither Darwinism nor Lamarcism offers an adequate explanation of their origin ; the evidence for other methods is, however, little more conclusive and is only of a general nature.

How isolated fragments of a variable population can become morphologically and physiologically distinct, independently of any kind of environmental selection, has been made clear by A. L. and A. C. Hagedoorn (quoted in Du Rietz, 1930). When a population colonizes an area and becomes geographically divided, even though the parts are isolated under similar conditions, the reduction of variability in these will probably lead to different results : the original composition of the parts is not likely to be exactly the same, and even if a certain gene is at first equally represented in all parts its fate in these will be largely determined by chance, possibly becoming eliminated from one population, but present throughout another. This automatic differentiation may, as Du Rietz points out, be increased and directed by isolation under different environmental conditions. The species of section *Rhizophyllum* seem to have been differentiated in this way, *E. Perralderianum* of Algeria differing from *E. pinnatum* of the Caucasus principally by the constant lack of a character, the power of forming leaves with more than three leaflets, which together with their firmer texture may be related to its drier habitat. The extent, however, to which isolation alone can influence specific differentiation must depend upon the stage of 'down-grade evolution' or stability already reached by the population becoming divided. Obviously a population may attain a state so uniform that, however long thereafter parts may be isolated, its potentialities of variation will be too slight for any appreciable divergence to take place. Probably many species of *Epimedium* are now in this state.

One example must suffice. No species has a range exceeding 1000 miles east to west or 500 miles north to south. *E. pubigerum*, spread from east Bulgaria to the west Caucasus, is accordingly one of the most widely ranging. It is now in cultivation from extreme stations (Strandja, Istanbul, Trabzon), between which there has probably long ceased to be an exchange of genes by cross-fertilization such as might account for the uniformity of a small compact population; nevertheless, these plants appear indistinguishable. If then isolation be taken as a factor important in the differentiation of species from populations blessed with high variability and in a youthful stage of development, its feeble effect upon the populations of *Epimedium* section *Rhizophyllum* and associated *Abies*, *Cedrus*, and *Quercus* mentioned above suggests that before they were parted these had already come almost to the last stage in their development.

Although the formation of species and subspecies from an originally variable stock ('coenospecies') may thus be accounted for, still there remains the cardinal problem of how this arose. Whatever the inner cause may be, there can be little doubt that certain features which are confined to one or two species, and sharply distinguish them from near allies, have arisen suddenly, i.e. as mutations, making new morphological departures for the group. To this category belong the remarkable stamens (twice as long as those of any other *Epimedium*) of *E. Fargesii*, which vegetatively is hard to tell from certain other Chinese species, and the glandular ovary of *Vancouveria hexandra* and *V. chrysanthra*, this being glabrous in *V. planipetala* and *Epimedium* proper. If such characters have arisen by mutation, then more widely distributed characters probably originated likewise. Although interspecific crossing has certainly taken place in gardens (cf. pp. 513-525), to what extent, if any, this has contributed to the diversity of the group in nature is doubtful. *Vancouveria* supplies a possible example. The Pacific coast of North America, to which *Vancouveria* is confined, has at various periods been subjected to upheavals and sinkings with incursions of the sea breaking it into independent areas. During this eventful geological past, the original *Vancouveria* stock probably became divided into a northern species (*V. hexandra*) and a southern species (*V. planipetala*); the third species (*V. chrysanthra*), occurring only where they overlap and combining their characters, may have arisen from their meeting and hybridization in more recent times.

Thus on general evidence *Epimedium* (sensu lato) appears to be a very old group, which probably originated in the early Tertiary temperate mixed forest-belt of northern Asia, and by the end of the Tertiary era had acquired a wide range across the northern hemisphere, remaining everywhere restricted to temperate woodland conditions. That range was broken by the Quaternary glaciation and the drying up of central Asia and the Mediterranean lands. This accords with the view that endemism of genera represents in most instances a juvenile generic condition, continuity over a wide area, a mature or optimal condition and discontinuity, of which *Epimedium* provides so good an example, a senile or diminishing condition. The haploid chromosome number for

Epimedium and *Vancouveria* is 6, as also for *Jeffersonia*, *Plagiorhegma*, and *Diphylleia* (Langlet, 1928), though 7 in *Ranzania* and 10 in *Nandina* (Miyaji, 1930); no cytological irregularities have been observed in the hybrids, due probably to the cytological uniformity of the parent species. Dermen (1931) and Giffen (1937) have found a like uniformity in *Berberis* and *Mahonia*; in all forms studied, except the tetraploid *B. turcomanica* var. *integerrima*, the haploid number was 14; the numerous and widespread species of these genera exhibit no important differences either in chromosome number or size. Dermen concludes that 'species differentiation in *Berberis* is not due to changes in chromosome number or to any fundamental change in chromosome structure or genetic constitution. Most of the differences between species are those which might be attributed to mutation associated with geographic isolation the production of polyploid types or fundamental change in the chromosome complex, produced by wide species hybridization, has evidently not played an important part in the formation of species in *Berberis*'. This conclusion seems equally applicable to *Epimedium* and other herbaceous Berberidaceae.

THE SPECIES IN CULTIVATION.

Cultivation creates experimental environments for plants and sheds light on climatic conditions which limit their dispersal. All the forms of *Epimedium* and *Vancouveria* being woodland plants thrive best, when in a garden, under cool, shady, and sheltered conditions, preferably in moist leafy soil. All are hardy in Britain and easy to grow, but are liable to have their flowers and first leaves damaged by frost or drying winds. They can be used for glasshouse decoration in March, by lifting clumps from the outdoor garden in December or earlier, potting in mingled loam, leaf-mould, and sand with the rhizomes about $\frac{1}{2}$ inch below the surface, and keeping moist and draught-free under a staging until the shoots are uncurling; a low temperature, about 45° F. or 8° C., is best. They are propagated by division of the rhizomes in autumn or as they begin to grow in late winter. The elegance of their leaves and delicate yellow, white, pink, carmine, or violet blossoms and their accommodating ways make them excellent for furnishing shady ledges of the rock garden and between shrubs and trees. Among the best are *E. pinnatum* β *colchicum*, $\times E. warleyense$, $\times E. rubrum$, *E. grandiflorum* δ 'Rose-Queen', *E. pubigerum*, *E. Youngianum* γ *niveum*, *V. chrysanthia*, and *V. hexandra*; *E. alpinum* is too vigorous, except for shrubberies. In sheltered positions, the leaves of *E. pinnatum* β *colchicum*, *E. Perralderianum*, *E. pubigerum*, *E. sagittatum*, and *V. planipetala* are evergreen and may be so in $\times E. versicolor$ δ *neo-sulphureum* and γ *sulphureum*, the commonest of all Epimedums in gardens; when young the leaves of many, notably *E. Perralderianum*, $\times E. rubrum$ and $\times E. versicolor$ α *versicolor*, are attractively marbled with red-brown and may assume bright reddish or yellow colours as they die in autumn. The flowering season of *Epimedium* is from late March (e.g. *E. pinnatum* β *colchicum*) to early June (*E. diphyllum*, $\times E. Youngianum$ γ *niveum*), with most kinds flowering in April, but of *Vancouveria* from late May to early July.

Although slugs, snails, rabbits, and occasionally leaf-cutter bees (*Megachile* sp.; cf. Wehrhahn in *Gartenflora*, LXXX, 297-99; 1931) attack Epimediums as they do other plants, there are no special pests of the genus at present known. The yellow mottling which disfigures some stocks, particularly of *E. alpinum*, seems due to an undescribed virus disease best countered by burning plants affected or growing them apart from others and not distributing.

For fungi recorded on *Epimedium*, see Saccardo, *Sylloge* (1882-1931).

A key to the cultivated species and hybrids of Epimedium.

1. Flowering stems leafless
- Flowering stem bearing 1 or more leaves
- Flowering stems leafy or leafless on the same plant
2. Petals very small, much shorter than the petal-like conspicuous inner sepals; laminae almost absent, 2-3 mm. high; spurs not exceeding 4 mm. long, brown or yellow.
Stamens protruding
- Petals conspicuous, often as long as the inner sepals; laminae distinct, petaloid, forming a cup 5 mm. high around the stamens; spurs cylindric-tapering, 6-9 mm. long. Stamens usually included. Flowering stems leafy or leafless on the same plant. Inner sepals broadly ovate, pale yellow in clon γ *sulphureum* and δ *neo-sulphureum*, rose in clon α *versicolor*, coppery in clon β *cupreum*. (Hybrids between *E. grandiflorum* and *E. pinnatum*)
3. Flowering stem always leafless. Inner sepals yellow
- Flowering stem frequently leafy. Inner sepals at first red, changing to copper. Petals with bilobed but not lacerated laminae. Anthers greenish. (Probably *E. alpinum* \times *E. pinnatum* β *colchicum*)
4. Leaves with 3, 5, or 9 leaflets often sparsely spinous or even entire at the margin
- Leaves with 3 (or 1) leaflets, never more, very spinous and undulate at the margin (the spines 0.5-1.5 mm. long, averaging 1.1 mm. long), the veins appearing pale and very evident on the upper surface against the darker green surrounding tissue. Spur of petal scarcely 2 mm. long, bent upward at an angle of about 45° from the lamina
5. Leaves often with 9 leaflets, though sometimes with 5 or 3 leaflets. Petals minute, 2 mm. long, the spur scarcely 1 mm. long
- Leaves with 3 or 5 (never 9) leaflets. Petals about 4 mm. long, the spur 2 mm. long
6. Leaflets sparsely spinous or sometimes even spineless at the margin (the spines 0.1-0.9 mm. long, averaging 0.5 mm. long). Spur of petal straight, projecting at about 90° from the lamina
- Leaflets usually distinctly spinous at the margin (the spines 0.2-2.5 mm. long), of firmer texture with more evident veining on the upper surface than in *E. pinnatum* β *colchicum*. Spur of petal slightly upcurved. (*E. Perralderianum* \times *E. pinnatum* β *colchicum*)
- 2.
7. [$\times E. warleyense$.
 $\times E. versicolor$ and]
- 3.
- $\times E. versicolor$.
4.
- $\times E. warleyense$.
5.
- E. Perralderianum*.
[α *originarium*.
E. pinnatum subsp.]
- 6.
- [β *colchicum*.
E. pinnatum subsp.]
- $\times E. Perral-chicum$.

7. Flowering stem normally with only 1 leaf, formed of 2 or several leaflets.....

Flowering stem with 2 (rarely 3) opposite 3-foliate leaves ; mature leaflets with minute appressed bristle-like hairs on the lower side. Flowers very small, less than 1 cm. across.

Stamens protruding

8.

E. sagittatum.

8. Flowers large, 3-5 cm. across. Spur of petal fine and slender, exceeding the inner sepal, up to 2.5 cm. long ; petal white in f. α *normale*, violet in f. γ *violaceum*, sulphur in f. β *flavescens*, carmine-rose in f. δ 'Rose-Queen'

Flowers small or medium-sized, 1-2.5 cm. across. Spur of petal absent or shorter than inner sepal when present ...

9.

Spur of petal cylindric, blunt, yellowish or yellow. Stamens protruding or in $\times E. rubrum$ and $\times E. versicolor$ sometimes just enclosed by the petals. Leaves usually with 5 or 9 leaflets spinous at margin

Petal spurless, flat, obovate, white. Stamens included, much shorter than the petals. Leaves normally with only 2 nearly spineless leaflets. Plant small

Petal spurless or spurred, obovate, white or pink, the spur varying even on one plant from being short and conical to being slender, sharp, and \pm equalling the inner sepal.

Stamens included, much shorter than the petals. Leaves variable, with 2, 3, 4, 5, 6, or 9 leaflets. (*E. diphylum* $\times E. grandiflorum$)

12.

E. diphylum.

10. Leaflets blunt or acute, but not acuminate, from 2-9. Inflorescence usually overtopping the stem-leaf, loose ; pedicels 5 mm. to 4 cm. long

Leaflets acuminate, usually 9. Inflorescence shorter than the stem-leaf, with the 3-8 greenish-white flowers rather crowded at the tip ; pedicels usually less than 1 cm. long...

11.

11. Flowers rose-lilac.....

Flowers white

12. Spur of petal with lamina reduced or absent. Stamens protruding

Spur of petal with distinct lamina. Stamens included.

Flowers \pm 2 cm. across

13.

13. Inner sepal dark crimson or yellowish white tinged with pink but not coppery, slightly longer than the slipper-like petal.

Filaments \pm 1 mm. long ; anthers yellow

Inner sepal coppery red (mingled red and yellow), twice as long as the petal. Filaments \pm 2 mm. long ; anthers greenish.

(Probably *E. alpinum* $\times E. pinnatum$ β *colchicum*.)

14.

14. Flowers 0.9-1.3 cm. across. Inflorescence very glandular ..

Flowers 1.8-2.5 cm. across. Inflorescence sparsely hairy or glabrous. Inner sepals bright crimson. Petals often with slight or distinct laminae tending to enclose the stamens.

(*E. alpinum* $\times E. grandiflorum$.)

15.

E. warleyense.

15. Rhizome elongated, slender. Mature leaflets sparsely pubescent or glabrous beneath, perishing in autumn. Inflorescence shorter than the stem-leaf. Inner sepals dark red ..

E. rubrum.

E. alpinum.

Rhizome compact, stout. Mature leaflets finely pubescent beneath, evergreen. Inflorescence overtopping the stem-leaf.
Inner sepals rose-tinged or almost white *E. pubigerum*.

16. Inflorescence simple. Inner sepals broadly ovate, flat, pale yellow, copper, or dull rose. (*E. grandiflorum* × *E. pinnatum*)
Inflorescence compound. Inner sepals narrowly ovate, boat-shaped, bright crimson. (*E. alpinum* × *E. grandiflorum*).

17. Inner sepal pale yellow; petal brighter yellow
Inner sepal rose ('old rose')
Inner sepal coppery

18. Stem leaf usually with 9 leaflets (rarely 5); basal leaves with 5–11 (usually 9) leaflets. Spur of petal often about as long as inner sepal
Stem leaf usually with 3 leaflets (occasionally 5); basal leaves with 3–9 (usually 3) leaflets. Spur of petal shorter by 3–5 mm. than inner sepal.....

× *E. rubrum*.
18. [× *versicolor*.
× *E. versicolor* clon
× *E. versicolor*
 β *cupreum*.
 [γ *sulphureum*.
× *E. versicolor* clon
 δ *neo-sulphureum*.
× *E. versicolor* clon

The application of the horticultural nomina nuda, *E. album*, *E. diffusum*, *E. Rawsonii*, *E. rectum*, *E. triphyllum*, listed in W. Robinson, Cat. Hardy Perennials, p. 24 (1871), is unknown to me.

ENUMERATION.

A note on nomenclature.—The nomenclature accords with the Vienna (1905) International Rules, ed. Briquet, as amended at Brussels (1910) and Cambridge (1930). I have found it convenient to distinguish three systematic categories:—species, subspecies, and forma. The term 'varietas' is not employed, because as others have already noted, the current indiscriminate application of this term to all subdivisions of species and hybrids has deprived it of definite scientific meaning, although it still remains a useful non-committal term for general purposes. For the designation of garden hybrids I have used, in a collective sense embracing all the plants resulting from the crossing of two species, the earliest binary ('specific') name applied to a member of that hybrid group; the individual members when horticulturally distinct are each given ternary ('varietal') names with 'clon' rather than 'var.' as a term of interpolation between the first and second epithets since these plants owe their persistence and distribution in gardens to vegetative propagation.

Misapplied names resulting from misidentifications are cited in inverted commas to distinguish them from homonyms. Thus the citation '*E. macranthum*' H. Lév. indicates that this was not a new name published by Léveillé in ignorance of *E. macranthum* Morr. & Dene, but merely a misapplication of a name already published by Morren and Decaisne; Léveillé erroneously thought he was using Morren and Decaisne's name correctly.

Place-names may be mentioned here, since synonyms, homonyms, and orthographic variants of these cause the student of geographical distribution as much trouble as do their counterparts among plant-names. Considerable difficulty is found in locating on maps the places in Asia named on herbarium

labels. This is partly because the places are often obscure, but even more often because Chinese, English, French, German, Italian, and Russian collectors render the same sound in different ways. Thus Szechwan is also spelled Sichuen, Setschwan, Se Tchouen, Seczuan, Ssu-Ch'uan, Sutchuen, Szeciuán, Szuchuan ; Tatsienlu may be Dadjenlou, Dadsianlu, Tarsond, Tachienlu ; Kweichow may be Cwei-ceu, Kouichou, Kouy-Tchéou, Kweichau, or Guidschou, this name being borne by a province and a town in another province (Szechwan) of China. Whenever possible the standardized lists issued by the Royal Geographical Society of London have been followed ; herbarium labels are copied literally when citing specimens. For locating places visited by David, Delavay, Farges, Potanin, and other collectors before 1898, Bretschneider's monumental *History* (1898) and map are invaluable. Effort, not always successful, has been made to ascertain the exact provenance of every specimen cited in this monograph and from detailed large-scale maps marked with these the maps above (all re-drawn in 1937), showing the general distribution of species and subspecies, have been reduced.

Abbreviations used in the following pages.

In the citation of specimens the following abbreviations are employed for the principal herbaria consulted (cf. pp. 410-411), etc. :—

- B.=Berlin-Dahlem ;
- B.M.=British Museum, South Kensington ;
- Boiss.=Herb. Barbey-Boissier, Geneva ;
- Cantab.=Cambridge, England ;
- D.U. Prag.=Deutsche Universität, Prague ;
- E.=Edinburgh ;
- F.=Florence ;
- Fan M.I.=Fan Memorial Institute of Biology, Peiping ;
- Gen.=Conservatoire de Botanique, Geneva ;
- G.H.=Gray Herbarium, Harvard ;
- K.=Kew ;
- L.=Leningrad, formerly Petrograd ;
- N.Y.=New York ;
- P.=Paris ;
- Sci. Soc. Nanking=Biological Laboratory of the Science Society of China, Nanking ;
- Stearn=author's private collection ;
- Sun Yat. Univ.=Botanical Institute of Sun Yatsen University, Canton ;
- U.S.N.H.=United States Nat. Herb., Washington ;
- V.=Naturhist. Museum, Wien.
- !=specimen seen by the present author ; the citation :—*E. platypetalum* K. Mey. (!), and similar citations with the exclamation-mark following an authority, indicates that type or authenticated specimens have been examined.
- *=illustration in colour ;
- fide L.R.A.=according to information supplied by Dr. L. R. Abrams.

VANCOUVERIA †.

VANCOUVERIA Morr. & Dene in Ann. Sci. Nat., Bot., ser. 2, II, p. 351 (1834); Endl. Gen. 853, no. 4812 (1839); Torr. & Gray, Fl. N. Am. I, p. 52 (1838); Benth. & Hook. f. Gen. Pl. I, p. 44 (1862); Brewer & S. Wats. Bot. Calif. I, p. 15 (1876); Robinson in A. Gray, Syn. Fl. N. Am. I, part 1, p. 71 (1895); Howell, Fl. Northwest Am. p. 28 (1897); Jepson, Fl. West. Mid. Calif. p. 204 (1901); Piper & Beattie, Fl. Northwest Coast, p. 164 (1915); Jepson, Fl. Calif., VII, p. 550 (1922), and Man. Fl. Pl. Calif. p. 395 (1925). *Sculeria* § Rafin., Fl. Tellur. II, p. 52, no. 188 (1837); non *Scouleria* Hook. (1829); *Epimedium*, sect. *Vancouveria* Baill., Hist. Pl. III, p. 56 (1871); Franch. in Bull. Soc. Bot. France, XXXIII, p. 41 (1886); Prantl in Engl. & Prantl, Pflanzenfam., III, 2, p. 76 (1888); Komarov in Acta Hort. Petrop. XXIX, p. 140, pro subgen. (1908); Himmelbaur in Denkschr. Akad. Math.-Nat. Wien, LXXXIX, p. 744 (1915).

Type-species:—*V. hexandra* (Hook.) Morr. & Dene (*S. geminata* Rafin.).

Flores trimeri: sepala interiora, petala, stamina 6.—*Herbae* perennes, pilis multicellularibus instructae. *Rhizoma* repens. *Folia* normaliter omnia basalia, composita, foliolis ad marginem haud spinosis. *Caulis* florifer normaliter aphyllus; *inflorescentia* multiflora, paniculata. *Flores* albi vel flavi, minutti vel parvi, 6–13 mm. longi. *Sepala exteriora* 6–9, bracteiformia, mox decidua, extrema minima. *Sepala interiora* reflexa, petaloidea, anguste obovata. *Petala* reflexa, unguiculata, apice cucullata vel plana, nectarifera. *Stamina* erecta; *antherae* valvulis 2 sursum dehiscentes. *Pistillum* 1, stylo elongato tenui; *ovula* ☿ vel pauca, biserialia. *Capsula* bivalvis; *semina* semi-orbicularia, arillata.—*Species* 3, Americæ boreali-occidentalis incolae.

Perennial herbs. *Rhizome* horizontally creeping, elongated, slender, furnished with brown membranous bracts. *Leaves* normally basal, usually biennial, sometimes 3- or 5-foliolate; *stipules* united into a membranous ligulate sheath; *petioles* terete; *leaflets* pilose above (when young) or glabrous above, cordate at base, indented and rounded at the tip, spineless but often undulate or crisped at the margin, usually obscurely 3-lobed. *Flowering stem* normally leafless, sometimes bearing one leaf in *V. hexandra*; *inflorescence* simple or compound, few- or many-flowered, glabrous or glandular. *Flowers* trimerous, regular,

† The name commemorates the English seaman, George Vancouver (1757–98), who, as Captain of His Britannic Majesty's Ship 'Discovery', surveyed the Pacific coast of North America in 1792; cf. G. Godwin, 'Vancouver, a life' (London, 1930). 'Vancouver' is an anglicized form of 'van Couverden' (from Couvorden in Holland), the Vancouver family being of Anglo-Dutch descent; Vancouver himself was born at King's Lynn, Norfolk, and is buried at Petersham in Surrey. The dedication of the genus to Capt. Vancouver was no doubt suggested by Douglas' type-material having been collected near Fort Vancouver on the Columbia River.

§ Named in honour of Dr. John Scouler (1804–71), who collected with Douglas in north-west America in 1825.

pendulous, glabrous or glandular, white or yellow; aestivation imbricate; parts free, opposite. *Outer sepals* ('sepals', A. Gray) 6–9, small, unequal, the inner larger, glabrous or glandular, soon falling. *Inner sepals* ('petals', A. Gray) 6, petaloid, spatulate, reflexing, c. 4–9 mm. long. *Petals* ('nectaries', A. Gray), 6, quite flat and lobed at the tip in *V. planipetala* but with a narrowly oblong stalk expanded and folded over at the tip as a nectariferous pouch in *V. hexandra* and *V. chrysanthra*, slightly shorter than the inner sepals, reflexing. *Stamens* 6, connivent; *filaments* glabrous or glandular, without appendages; *anthers* about as long as the filaments, dehiscing by two oblong valves. *Ovary* glabrous or glandular; *ovules* two or several; *style* slender, with a slightly dilated *stigma*. *Capsule* splitting to the base as two valves. *Seeds* smooth, almost black, about 3 mm. long, semi-orbicular when viewed laterally before removal of the conspicuous aril.

Distribution.—Pacific coast States of NORTH AMERICA, from north WASHINGTON to middle CALIFORNIA.

CLAVIS VANCOUVERIAE SPECIERUM.

Folia tenuiter membranacea, autumno decidentia, foliolis ad margines planis neque duris. Pedicelli glabri: . . .	
Flores albi \pm 1–3 cm. longi; petala (nectaria) ad apices cucullata; sepala exteriora, stamina, ovarium glandulosa. Capsula usque ad 1·5 cm. longa	1. <i>V. hexandra</i> .
Folia rigide subcoriacea, per hiemem permanentia, foliolis ad margines duratis saepe crispis. Pedicelli glandulosi: . . .	
Flores flavi \pm 1–1·3 cm. longi; petala ad apices cucullata; sepala exteriora, stamina, ovarium glandulosa. Capsula . . . Inflorescentia pauciflora (floribus 6–18), plerumque subsimplex .	2. <i>V. chrysanthra</i> .
Flores albi \pm 6–8 mm. longi; petala plana ad apices lobata sed haud cucullata; sepala exteriora, stamina, ovarium glabra. Capsula usque ad 6 mm. longa. Inflorescentia multiflora (floribus 20–50), plerumque laxe paniculata	3. <i>V. planipetala</i> .

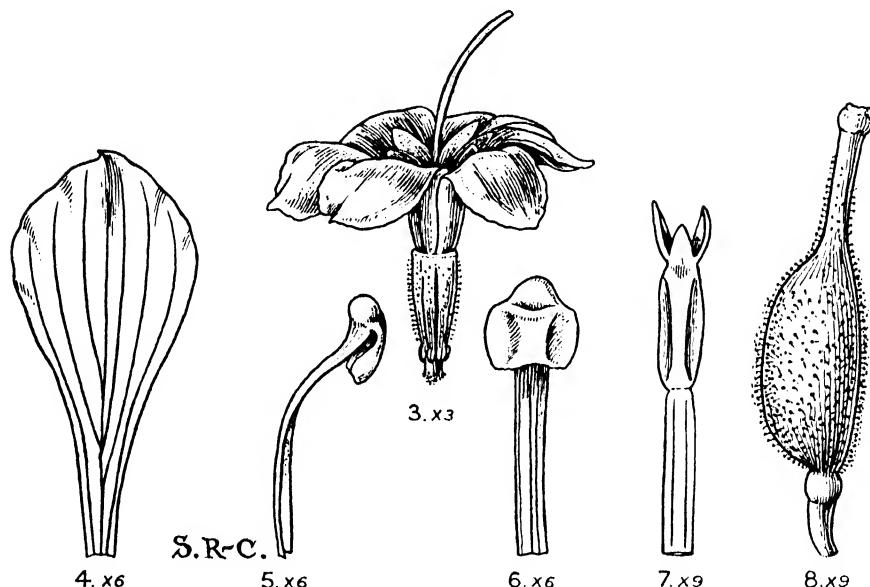
ENUMERATIO VANCOUVERIAE SPECIERUM.

1. *V. HEXANDRA* (Hooker) Morren & Decaisne. (Pl. 24.)
Epimedium hexandrum Hook. (!) Fl. Bor. Am. I, p. 30, t. 13 (1829): Seringe, Bull. Bot., no. 3, p. 69, t. 5, fig. O (1830): Franch. in Bull. Soc. Bot. France, XXXIII, p. 112 p.p. (1886): Komarov in Acta Hort. Petrop. XXIX, p. 140 (1908), excl. syn. 'V. planipetala'. *Caulophyllum gracile* Douglas (!) ex Hook., loc. cit. pro syn. (1829). *Vancouveria hexandra* (Hook.) Morr. & Dene in Ann. Sci. Nat. Bot., ser. 2, II, p. 351 (1833): Torr. & Gray, Fl. N. Am. I, p. 52 (1838): Brewer & S. Wats., Bot. Calif. I, p. 15 p.p. (1876): auct. anon. in The Garden, XXX, p. 263 cum ic. (1886): Calloni in Malpighia, I, p. 266 (1887): Robinson in A. Gray, Syn. Fl. N. Am. I, pt. 1, p. 71 (1895): Howell, Fl. Northwest Am. p. 28 (1897); Piper, Fl. Wash. in Contrib. U.S. Nat. Herb. XI, p. 283 (1906): Piper & Beattie, Fl. Northwest Coast, p. 164 (1915): T. H.

Hubbard in L. H. Bailey, Stand. Cycl. Hort. vi, p. 3429 (1917) : Farrer, Engl. Rock Gard. II, p. 419 (1919) : Jepson, Fl. Calif. VII, p. 551 (1922) and Man. Fl. Pl. Calif. p. 396 (1925). *Sculeria geminata* Rafin. Fl. Tellur. II, p. 52 (1837). *V. brevicula* Greene (!) ex House in Muhlenbergia, IX, p. 91 (1914). ? *V. picta* Greene (!) in Fedde, Repert. Sp. Nov. XIII, p. 322 (1914), vide infra. *V. parvifolia* Greene (!) in Fedde, Repert. Sp. Nov. XIII, p. 323 (1914). ' *Caulophyllum* ? *thalictroides* ? ' Douglas, Journal, 1823-27, p. 118 (1914).

Figures.—Hook. Fl. Bor. Am. I, t. 13 ; The Garden, XXX, p. 263 (1886).

Plant in flower 10-40 cm. high. Rhizome long-creeping, 1-3 mm. thick but stouter at the tip. Leaves normally basal, bi- or tri-ternate, clothed



FIGS. 3-8.—Details of the flowers of *Vancouveria hexandra*. 3, a flower, $\times 3$; 4, an inner sepal, $\times 6$; 5 & 6, a petal, $\times 6$; 7 a stamen, $\times 9$; and 8, the gynoecium, $\times 9$.

when young with profuse white hairs ; leaflets narrowly ovate to broadly ovate or almost oblate, often three-lobed, the tip rounded and indented, the margin not cartilaginous crisped or spiny, the base cordate with rounded lobes, always thin and membranous in texture, perishing in autumn, bright green above, glaucescent beneath, at first pilose on both surfaces but becoming almost glabrous, very variable in size and shape, up to 7.5 cm. broad, 7 cm. long. Flowering stem leafless (or abnormally and rarely bearing one leaf), rising well above the foliage, pilose below but ending in a glabrous loose inflorescence of 6-45 flowers, the lower peduncles often 3- (sometimes 6-) flowered and up to 12 cm. long, the upper one-flowered ; pedicels glabrous, 1-3 cm. long, two or three sometimes arising together. Flowers white, becoming yellowish

on drying, 1-1·3 cm. long, pendulous, the reflexing sepals and petals and connivent stamens (as in other species) giving them a shuttlecock appearance. *Outer sepals* dotted with very short red glandular hairs, unequal, the outer very short, the inner up to 5 mm. long. *Inner sepals* spatulate, narrowing to a clawed base, slightly cuspidate at the tip, the margin undulate, 8-9 mm. long, towards the tip 3-4 mm. broad. *Petals* (nectaries) long-clawed, shorter than the inner sepals, the narrowly oblong stalk (or lamina) 5 mm. long and 1 mm. broad and expanded and folded over at the tip as a quadrate flap to form a rounded nectariferous pocket 1·5 mm. high, 2 mm. broad. *Stamens* 4 mm. long, sparingly glandular with very short red glands; filaments 2 mm. long. *Ovary* very glandular. *Capsule* about 1·5 cm. long, 1-4-seeded; seeds black, about 3 mm. long, 2 mm. broad, almost covered by the aril.

Distribution.—NORTH AMERICA, Pacific coast of the UNITED STATES, southwards from north Washington, across Oregon, to Mendocino county in middle California, inhabiting usually the dense shade of coniferous forest in the humid transition zone.

The exact type-locality of this species is uncertain. The specimen (K.!) from which Hooker's plate and most of his description seems to have been drawn, bears the note, 'common in shady pine-woods at Fort Vancouver, Puget Sound and N. California', and was collected by David Douglas, probably near Vancouver (now a city) in May 1825 not long after McLoughlin's foundation of the Hudson's Bay Co. fort there; other Douglas specimens are in the Cambridge herbarium and the British Museum (!). Menzies' specimen (in K.!) is not the type; Menzies' material (B.M.!), is labelled on the back of the sheet from the 'Northwest coast of America, New Georgia' (this corresponding nowadays to the western part of the State of Washington, U.S.A., and the south of British Columbia†) and was probably collected late in May 1792 near Olympia.

Brewer and Watson (1876) describe *V. hexandra* as 'ranging from Santa Cruz to Vancouver Island'; this record is repeated in Macoun (Cat. Canad. Pl. I, p. 30; 1883), but needs confirmation. There are no specimens from Canada in the Gray Herbarium and the other collections I have examined; moreover, Prof. John Davidson of Vancouver, B.C., and the late Dr. M. O. Malte of Ottawa have both informed me they have seen no Canadian material. *V. hexandra* thus seems to have been recorded in error from British Columbia owing to confusion of Vancouver Island, B.C., with [Fort] Vancouver in the State of Washington, U.S.A.

† See map in W. J. Hooker, Fl. Boreali-Am. I (1829), or G. Goodwin, Vancouver, a life (1830). Menzies' specimens, being partly in bud, were collected probably in late May. From May to June in 1793 and 1794 Vancouver's ships were off the British Columbian and Alaskan coasts, too far north for *Vancouveria*, but in May 1792 they explored Puget Sound, reaching the site of Olympia on May 26, and Menzies' Journal shows that he went ashore to collect in this neighbourhood on May 28 and 31. On June 5 Vancouver sailed out of Puget Sound for ever.

WASHINGTON. Chehalis Co.:—Chehalis River [Preacher's Slough, fide L.R.A.], *Lamb* 1247 (N.Y. ! K. ! Boiss. !). Pierce Co.:—Common in woods, upper valley of the Nesqually, 1894, *Allen* 66 (N.Y. ! G. ! U.S.N.H. ! K. ! B.M. !). deep woods, Nisqually River, *Piper* 2059 (U.S.N.H. !); Ashford, *Cowles* 637 (G.H. !). Thurston Co.:—Common in open woods, Olympia, 24. v. 1892 (fl.), 12. vi. 1892 (fr.), *Henderson* (Seattle !), Olympia, 31. v. 1908, *Bailey* (Seattle !). Pierce Co.:—Goose Lake, Mount Rainier Forest Reserve, *Flett* (U.S.N.H. !); moist shady place near Mount Rainier, alt. 2500 ft., 1896, *Flett* (U.S.N.H. !). Clarke Co.:—Fort Vancouver, *Scouler* (? type, K. !); Vancouver Barracks, *Mearne* (U.S.N.H. !), *Willcox* (G. !); Vancouver, *Ebert* (U.S.N.H. !), *Piper* 4921 (U.S.N.H. !); Columbia river, 1825, *Douglas* (Cantab. !). Skamania Co.:—Cape Horn (fide *Piper*, loc. cit., 1908). Klickitat Co. (west):—Damp woods, 1884, *Suksdorf* (N.Y. ! U.S.N.H. ! P. ! Boiss. ! B.M. !).

OREGON. Multnomah Co.:—McLeay Park, Portland, 1902, *Sheldon* 10480 (N.Y. ! U.S.N.H. ! G. ! K. !); moist woods, E. Portland, *Thompson* 856 (K. !); ravine slope, common, vicinity of Portland, *Palmer* 1468 (N.Y. ! U.S.N.H. !); Portland, *Piper* 6188 (U.S.N.H. !); in dense woods at Portland, *Lunnell* (N.Y. ! K. !); vicinity of Bonneville, *Lyon, Jr.* 48 (N.Y. ! U.S.N.H. !). Washington Co.:—Forest Grove, 1893, *Lloyd* (N.Y. !) *Marsh* (Seattle !); moist shade, Scroggins Creek, *Thompson* 4299 (U.S.N.H. !). Hood River Co.:—Coniferous forests, base of Mt. Defiance, *Henderson* (fide L.R.A.). Clackamas Co.:—Moist woods, Oregon City, *Thompson* 682 (K. !); Eagle Creek, *Abrams* 8816 (fide L.R.A.). Marion Co.:—Gravelly woods, Salem, *Nelson* 1276 (G. !); wooded hillside near Turner, *Nelson* 99 (fide L.R.A.). Benton Co.:—Coast mount foot-hills, Sulfur Springs west of Corvallis, *Laurence* 1696 (fide L.R.A.). Douglas Co.:—Oakland, *Wood* (N.Y. !); Stage Road Pass, Pacific Highway, *Abrams & Benso* 10454 (fide L.R.A.). Coos Co.:—Rocky banks, head of Coos River, *House* 4832 (U.S.N.H. ! type-no. of *V. brevicula*). Curry Co.:—Rogue River, *Austin* 1508 (U.S.N.H. !); in the shade by roadside, Gold Beach, *Hoyt* 87 (N.Y. !); Brookings, *Thompson* 134 (fide L.R.A.); low thicket, Cape Blanco, *Peck* 8557 (N.Y. ! G. !). Josephine Co.:—Dry woods, Grant's Pass, *Prescott* (G. !); Oregon Caves, trail top of Lake Mount, *Kildale* (fide L.R.A.). Jackson Co.:—In moist woods along Antelope Creek [10 miles east of Medford], alt. 2300 ft., *Applegate* 2358 (U.S.N.H. !); west slope, Cascade Mts., moist woods, *Applegate* 19 (U.S. N.H. !); High Cascades 30 miles east of Medford, *Heckner* (K. !); Sykes Creek, near Wimer, *Hammond* 15 (N.Y. ! U.S.N.H. !); Dead Indian road, head of Walker Creek, shady coniferous woods, *Applegate* 19 (fide L.R.A.); Grizzly Peak, north-east of Ashland, 4500 ft., *Mason* 4061 (hb. Stearn ! ex Herb. Univ. Calif.). Klamath Co.:—Lake of the Woods [30 miles northwest of Klamath Falls], in fir woods, *Coville & Applegate* 82 (U.S.N.H. !), *Applegate* (U.S.N.H. !).

CALIFORNIA. Del Norte Co.:—Trail up Klamath River to Blue Creek, *Kildale* 8428 (fide L.R.A.). Siskiyou Co.:—Happy Camp, Waldo (Oregon)

Road, watershed of west branch of Indian Creek, Klamath National Park, 1934, *Lee* 1083 (hb. Stearn ! ex Univ. Calif.). Humboldt Co. :—Humboldt Bay, 100 ft., *Chandler* 1162 (U.S.N.H. !—type of *V. parvifolia* ; G. !; N.Y. ! P !), Frances Camp, *Smith* 3842 (U.S.N.H. ! G. ! N.Y. !); Grizzly Creek, *Abrams* 6150 (fide L.R.A.); Bull Creek Area, Humboldt Redwood Park, *Constance* 856 (hb. Stearn ! ex Univ. Calif.). Mendocino Co. :—Albion River, *McMurphy* 11 (U.S.N.H. ! N.Y. ! Gen. ! no. 11 a); Pudding Creek, 1894, *Eastwood* (G. !); Noyo River, *Hoak* (fide Jepson, loc. cit., 1922); between Blocksburg and Bridgeville, *Abrams* 5983 (U.S.N.H. ! N.Y. !).

This is the type of *Vancouveria*, having been collected first by Menzies (who was surgeon and naturalist aboard Vancouver's *Discovery*) and later by Douglas and Scouler. It is recognizable by its membranous leaflets, glabrous inflorescence, and glandular flower-bracts, stamens, and ovary. In 1914 Greene proposed three new ' species ', *V. brevicula*, *V. parvifolia* and *V. picta*, using characters of doubtful value. *V. parvifolia* is only a state with small leaflets which can be produced from typical *V. hexandra* by growing it under dry conditions; that the type-specimens are immature is shown by the hairs still present on the upper surface of the leaflets of *Chandler* no. 1162 in the Paris herbarium, while the same gathering in the New York herbarium has leaflets up to 5 cm. broad and 4·5 cm. long. *V. brevicula*, collected at the head of the Coos River in September, was distinguished by its small leaflets and late flowering, although this, according to House, may be ' merely a rejuvenescence, due to the warm autumnal rains, such as occurs in this region in the case of *Trifolium*, *Mimulus*, *Mitella*, and many other herbaceous vernal plants '. *V. picta* also seems to be only a state of *V. hexandra* having mottled young leaflets (observable in many Epimedums under cultivation) distinctly trilobed, but as on a few pedicels there are scattered hairs its status is more debatable; it may deserve varietal recognition.

Farrer has aptly described *V. hexandra* as ' a most beautiful *Epimedium*, with the ample leafletted leafage of the race, soft bright-green in colour, and much more graceful, wide, airy, and light in habit than any of the others. The flowers, which are small and creamy, come up in summer on stems of 10 inches or a foot, in the most delicate and dainty loose showers, so that each little star seems to float pendulous on the air by itself '. It is easily cultivated under shady conditions in light moist soil and was introduced into European gardens sometime before 1886.

2. V. CHRYSANTHA Greene. (Pl. 24.)

V. chrysantha Greene (!) in Bull. Calif. Acad. Sci. I, p. 66 (1885) : Robinson in A. Gray, Syn. Fl. Am. I, pt. 1, p. 71 (1895) : Howell, Fl. Northwest Am. p. 28 (1897) : Barclay in L. H. Bailey, Cycl. Am. Hort. IV, p. 1897 (1902) : T. H. Hubbard in L. H. Bailey, Stand. Cycl. Hort. VI, p. 3429 (1917) : Gabrielson, West. Am. Alpines, p. 254 (1932) : Rowntree, Hardy Californians, p. 158

(1936). *V. hexandra* var. *aurea* Rattan, Analyt. Key West Coast Bot. p. 17 * (1887). *V. aurea* Greene ex Rattan, loc. cit. pro syn. (1887). *V. hexandra* var. *chrysanthra* (Greene, Greene, Pittonia, II, p. 100 (1890). *Epimedium chrysanthum* (Greene) Komarov in Acta Hort. Petrop. XXIX, p. 141 (1908), reimpr. in Fedde, Repert. Sp. Nov. VIII, p. 420 (1910).

Plant in flower 20–40 cm. high. Rhizome long-creeping, 2 mm. thick, but stouter at the tip. Leaves basal, biennial or 3- or 5-foliolate, the petioles and nodes more profusely clothed than in other species with slender spreading hairs; leaflets ovate to almost oblate (i.e. much broader than long), obscurely 3-lobed, the margin cartilaginous thickened and crisped, subcoriaceous in texture, and ‘almost evergreen’, dark green and glabrous above, glaucous and usually very pubescent beneath with numerous soft hairs, variable in size and shape, but up to 4 cm. long, 4 cm. broad. Flowering stem leafless, pilose below and ending in a very glandular loose inflorescence of 4–15 flowers, usually simple but the lower peduncles sometimes 2- or 3-flowered; pedicels glandular, up to 3 cm. long. Flowers ‘soft yellow’ (Gabrielsson) or ‘brilliant rich yellow’ (Rowntree), darkening on drying, 1–1·3 cm. long. Outer sepals glandular, unequal, the inner up to 4 mm. long. Inner sepals spatulate, narrowing to a clawed base, 7–8 mm. long, towards the rounded tip 3·5 mm. broad. Petals shorter than inner sepals, the narrowly oblong stalk about 4 mm. long and expanded and folded over at the tip to form a rounded nectariferous pocket 2 mm. high, 1 mm. broad. Stamens 4 mm. long, sparingly glandular; filaments 2 mm. long. Ovary glandular.

Distribution.—NORTH AMERICA, Pacific Coast, UNITED STATES. *V. chrysanthra* is at present represented in herbaria by only a few specimens from south-west Oregon, Josephine county, near the California boundary, and is evidently of much more limited range than *V. hexandra* and *V. planipetala*. Gabrielsson describes it as ‘a plant of the open, rocky hillsides of southern Oregon and northern California. There it grows about the base of the manzanita [*Arctostaphylos*] and California lilac (*Ceanothus*). Its leaves are thick, leathery, and almost evergreen, while the soft yellow flowers are larger and more conspicuous than [those of] *V. hexandra*’.

Type-locality.—‘Coast mountains of Oregon, on about the forty-second parallel, Thomas Howell, June 8, 1884’ (Greene, loc. cit., 1885).

OREGON. Coast mountains, fortieth parallel, 8. vi. 1884, T. Howell, Pacific Coast Plants, as *V. hexandra* var. *aurea* Wats. (U.S.N.H. ! N.Y. ! K. ! Gen. ! type-collection); dry rocky ground 10 miles SW. of Waldo, Josephine County, Thompson 4685 (U.S.N.H. ! K. !); eight miles south of Waldo, Piper 6123 (U.S.N.H. ! G. !); Illinois River, SW. Oregon, 10 miles from Waldo, Rattan (G. !); summit of Siskiyou Mts., south of Waldo, Thompson 472 (K. !).

* ‘*V. hexandra* M. & D. Panicle of white flowers on a scape. var. *aurea*. Flowers yellow, larger. S.W. Or. (v. *aurea* Greene)’ (Rattan, loc. cit.).

CALIFORNIA : no specimens seen, but Mrs. L. Rountree (in litt.) writes that she has found it 'in a few places, all in the Siskiyous, along the Oregon-California line, sometimes in one State, sometimes in the other, e.g. by the old stage-coach road which runs from Gasquet in Del Norte Co., Calif., into Oregon . . . also at some distance from the Happy Camp Road [Siskiyou Co.] which also leads across the State line . . . Every plant has been right in among low shrubs, Berberis, bracken, etc.'

This species differs from *V. hexandra* in its glandular pedicels and coriaceous leaves and from *V. planipetala* in its few-flowered inflorescence and larger flowers, in structure like those of *V. hexandra*, with hooded petals, glandular stamens, and ovary ; it is also more hairy and its leaflets usually fewer. The flowers are yellow, darkening on drying ; those of *V. hexandra* and *V. planipetala* are white when living, but may become yellowish on drying. *V. chrysanthia* occurs where the ranges of the other two species overlap and its extremely limited area and intermediate character suggest that it is a species of more recent origin which may have arisen from their hybridization.

Komarov cites a specimen 'e California sept. a dr. Wosnesensky lectam', which I have not been able to see ; if correctly identified, then E. Wosnesensky or Voznesenski, who collected in Pacific Coast North America (about 1840) for the Petrograd Academy of Sciences when the Russian Fur Company owned Fort Ross, Sonoma Co., Calif., should be credited with discovering the species.

C. chrysanthia is a newcomer to British gardens. A plant I received in 1932 failed to grow ; another, received by Dr. F. Stoker in 1935, has now established itself in his woodland garden at Loughton, Essex ; it should prove a good garden plant.

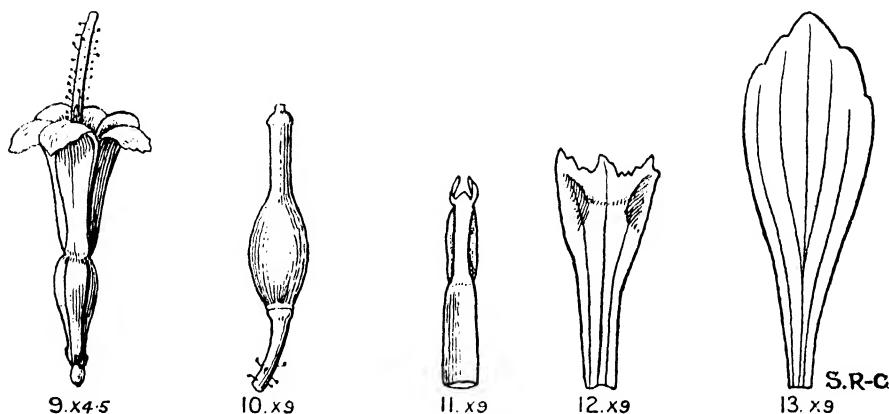
3. *V. PLANIPETALA* Calloni. (Pl. 25.)

'*V. hexandra* Morr. & Dene', secundum Brewer & S. Wats. Bot. Calif. I, p. 15, p.p. (1876), non Morr. & Dene : Greene in Bull. Calif. Acad. Sci. I, p. 66 (1885). '*Epimedium hexandrum* Hook.', secundum Franch. in Bull. Soc. Bot. France, XXXIII, p. 112, p.p. (1886), non Hook. *V. planipetala* Calloni (!) in Malpighia, I, pp. 263-72, t. 6 (1887) : [Stearn in] Kew Hand-list of Rock Gard. Pl., ed. 4, p. 149 (1934) : Clay, Present-day Rock Gard. p. 645 (1937). *V. parviflora* Greene (!), Pittonia, II, p. 100 (1890) : Robinson in A. Gray, Syn. Fl. N. Am. I, pt. 1, p. 71 (1895) : Parsons & Buck, Wild Fl. Calif. p. 88, cum ic. (1897) ; Armstrong, Field Book West. Wild Fl. p. 152, cum ic. (1915) : T. H. Hubbard in L. H. Bailey, Stand. Cycl. Hort. VI, p. 3492 (1917) : Jepson, Fl. Calif., VII, p. 551 (1922), and Man. Fl. Pl. Calif. p. 396 (1925). *E. planipetalum* Citerne, Berberid. Erythrosp. p. 21 (1892). *V. chrysanthia* var. *parviflora* (Greene) Jepson, Fl. West. Mid. Calif. p. 204 (1901). *E. parviflorum* (Greene) Komarov in Acta Hort. Petrop. XXIX, p. 141 (1908), reimpr. in Fedde, Repert. Sp. Nov. VIII, p. 420 (1910). *E. hexandrum* f. *planipetala* Himmelbaur in Denkschr. Akad. Math. Nat. Wien, LXXXIX, p. 744 (1914). *V. crispa*

Greene (!) in Fedde, Repert. Sp. Nov. XIII, p. 321 (1914). *V. Vascyi* Greene (!), l.c. (1914). *V. concolor* Greene (!) l.c. p. 322 (1914). ' *V. hexandra* . . . form or subspecies' Farrer, Engl. Rock Gard. II, p. 419 (1919). *V. hexandra* var. *sibirica* hort., Kew Handl. Rock Plants, ed. 3, p. 109 (1924), nomen nudum.

Figures.—*Malpighia*, I, t. 6 (1887); Parsons, Wild Fl. Calif. p. 89; Armstrong, Field Book, p. 153.

Plant in flower 18–32 cm. high. Rhizome long-creeping, 2–4 mm. thick, the leafy tips rising above the ground. Leaves basal, usually biternate, sometimes ternately compound with the three divisions 5-foliolate, or rarely simply 5-foliolate; leaflets broadly ovate, often broader than long and three-lobed, the margin cartilaginous thickened and slightly or much crisped, subcoriaceous and evergreen, dark glossy green and glabrous above, dull grey-green and glaucous beneath with short sparse hairs, very variable in size,



Figs. 9–13.—Details of the flower of *Vancouveria planipetala*. 9, a flower, $\times 4\frac{1}{2}$; 10, the gynoecium, $\times 9$; 11, a stamen, $\times 9$; 12, a petal, $\times 9$; and 13, an inner sepal, $\times 9$.

but up to 6 cm. broad, 5 cm. long. Flowering stem leafless, rising above the foliage, pilose below and ending in glandular loose panicle of about 20–50 flowers, the lower peduncles up to 15-flowered; pedicels glandular, 1–2 cm. long. Flowers white or lavender-tinged, 6–8 mm. long (including stamens and reflexed sepals). Outer sepals glabrous, unequal, the inner up to 3 mm. long. Inner sepals spatulate, narrowing to a clawed base, the margin erose, 4 mm. long, towards the tip 2 mm. broad. Petals shorter than the inner sepals, oblanceolate, flat and notched at the tip with a slight median lobe and larger yellow lateral lobes but not saccate, 3 mm. long, 1 mm. broad. Stamens 2 mm. long, glabrous; filaments about 1 mm. long. Ovary glabrous. Capsule 4–6 mm. long, one- or two-seeded; seeds black, 3–4 mm. long, 2 mm. broad.

Distribution.—NORTH AMERICA, Pacific coast UNITED STATES, from the Rogue River, Oregon to the Santa Lucia mountains of California.

Type-localities.—*V. planipetala*, ‘nei boschi ombrosi “paper mill red woods” presso S. Francisco di California, a circa 38° di lat. sett. dove Bolander la raccolse nel maggio 1867’ (Calloni, loc. cit.) ; *V. parviflora*, ‘common on bushy hills from the Santa Cruz Mountains northward to and beyond Mt. Tamalpais, California, flowering in May’ (Greene, loc. cit. 1890) ; *V. crispa* ‘collected somewhere in Mendocino County, California, 3 August 1902, by the late J. W. Congdon’ (Greene, loc. cit.; 1914) ; *V. concolor* ‘from the coast mountains back of Pescadero, San Mateo County, California, obtained in May 1903 [at Iverson’s Place by A. D. E. Elmer, no. 4922 !] and distributed for *V. parviflora*’ (Greene, loc. cit.; 1914) ; *V. Vaseyi*, ‘from some unknown station in some part of California collected by George Vasey Jr. in 1875’ (Greene, loc. cit.; 1914).

The first collector of this plant was David Douglas, but his specimen (B.M.! ex herb. Soc. Hort. Lond.), labelled ‘Nova California, 1833’, was referred to *V. hexandra* until determined by the present writer a hundred years later.

OREGON, south :—rocky woods along Rogue River near Mule Creek [Jackson Co.], 1917, Nelson (G.!).

CALIFORNIA. Del Norte Co.:—Rocky ledge 30 miles up Smith River near Gasquet, Thompson 4551 (K. ! U.S.N.H. !); Patrick’s Creek on Crescent City—Grants Pass Road, Abrams & Bacigalupi 8573 (fide L.R.A.); Shelley Creek, 1923, Eastwood (K.!). Humboldt Co.:—in redwoods near Grizzly Gulch, alt. 500 ft., Tracy 2678 (G. ! U.S.N.H. !); shaded woods, arid Transition Zone, Willow Creek, Abrams 7189 (fide L.R.A.); Sweasey Lake, McClellan Mt., Kildale 2192 (fide L.R.A.); Bull Creek Area, Humboldt Redwood Park, Constance (hb. Stearn! ex Univ. Calif.). Trinity Co.:—forested north slope between Mad and Trinity Rivers on Eureka—Red Bluff Road, Abrams 6201 (U.S.N.H. ! N.Y. !). Mendocino Co.:—Ukiah, Kellogg & Harford (N.Y. !); redwoods at Ukiah, Bolander 3910 (K. ! U.S.N.H. ! G. !); near Mendocino, below 500 ft., Brown 740 (U.S.N.H. ! N.Y. ! Gen. !); Kaisen District, McMurphy 10 (U.S.N.H. ! N.Y. ! Gen. !); Wolf Creek, alt. 1396 ft., Abrams 5888 (N.Y. !), sine loc. sp., 1867, H. N. Bolander (Boiss. !); Noyo River, Hoak (fide Jepson, loc. cit.; 1922); Comptche, Jones 28887 (B.M.!). Sonoma Co.:—Fort Ross, Heller (G. !); Santa Cruz Mts., to and beyond Mt. Tamalpais, Congdon (fide L.R.A.); Cazadero, R. Bacigalupi 1376 (fide L.R.A.). Napa Co.:—Calistoga, Redwood Peak (fide Jepson, loc. cit. 551, 1922). Marin Co.:—Paper mill red-woods, 5. v. 1867, Bolander (Gen. ! type of *V. planipetala* Calloni); redwoods E. of Paper Mill Creek, Bolander (P. ! Boiss. !); Mill Valley, Michener & Bioletti (U.S.N.H. ! Seattle !); Mount Tamalpais, Rydberg 6241 (N.Y. !); Lagunita Cr., Eastwood (G. !); Willow Camp, via Pipe-line, Rattlesnake and Steep Ravine, Mason 1131 (hb. Stearn! ex Univ. Calif.). San Mateo Co.:—Big Basin, 9. v. 1903, Copeland ex Baker 3051 (K. ! G. ! U.S.N.H. ! N.Y. ! Gen. ! authenticated by Greene as *V. parviflora*); Woodside, Walther (U.S.N.H. !); forest shade, King’s Mountain, Rose 32269 (K. !), Patterson (Mas. Univ. Brno !), Pescadero, v. 1903, A. D. E. Elmer 4922 (U.S. N.H. !—type of *V. concolor*; N.Y. ! B. ! Zürich !). Santa Cruz Co.:—

Glenwood, *Davis* (U.S.N.H. !); Camp Idle, Santa Cruz Mts., *Davis* (K. !). Big Basin, *Mason* 3382 (hb. Stearn ! ex Univ. Calif.). Santa Clara Co.: Lane, near Wrights, *Wolley-Dod* 166 (B.M. !). Monterey Co.:—Stevens Canon, Santa Lucia Mts., *Dudley* (fide L.R.A.).

V. planipetala is easily recognized by its firm leaflets, its glandular inflorescence and its minute, glabrous, white or lavender-tinged flowers. In England it has been cultivated for many years under the names '*V. sibirica*' and '*V. hexandra* var. *Buckhouisci*', being distributed by the nurserymen Backhouse of York; it is the plant mentioned by Farrer (1919) under *V. hexandra* as an evergreen 'form or subspecies which differs in having the leafage rather more condensed and leathery, especially beautifully goffered round the leaflets, and turning to shining red and russet on the upper surface, while the under side is of a contrasting glaucous-blue'.

The name *Vancouveria planipetala* has usually been treated as a synonym of *V. hexandra*, although Calloni's elaborate description and figure, the type-locality in California south of the range of *V. hexandra* and Bolander's type-gathering (herb. DC. at Gen. ! P. !) prove that it is the species which has become well known under the later name *V. parviflora*. In 1914 Greene described three more 'species', *V. Vaseyi* ('peculiar . . . by the glaucous hue of the upper face of its foliage and especially by its racemose inflorescence'), *V. concolor* ('with foliage too thin to be called leathery yet perfectly evergreen'), and *V. crispa* (with foliage 'much more hard leathery and all leaflets conspicuously and strongly crisped'). Comparison of the type-material reveals no floral differences and the vegetative characters adduced by Greene are so indefinite and merge to such an extent when a good range of material is examined that one can only treat these plants as states of one plastic species.

Mrs. A. Sherman Hoyt writes that in California the leaves of this *Vancouveria* ('Redwood Ivy' or 'Mexican Ivy') are 'picked in great numbers and shipped widely to florists' for decorative purposes.

EPIMEDIUM.

EPIMEDIUM [Tourn., Elemens Bot. I, p. 198 (1694), Inst. Rei Herb. p. 232, t. 117 (1700)] : Linn. Sp. Pl. p. 117 (1753), Gen. Pl., ed. 1, p. 30, no. 81 (1737), and ed. 5, p. 53, no. 138 (1754) : Endl. Gen. p. 853, no. 4811 (1839) : Spach, Hist. Veg. Phan. VIII, p. 55 (1839) : Hook. f. & Thoms. Fl. Ind. I, p. 231 (1855) : Benth. & Hook. f. Gen. Pl. I, p. 44 (1862) : Franch. in Bull. Soc. Bot. France, XXXIII, p. 103, p.p. (1886) : Prantl in Engl. & Prantl, Nat. Pflanzenfam., III, 2, p. 75, p.p. (1888) : Tischler in Engl. Bot. Jahrb. XXXI, p. 723, p.p. (1902) : N. Busch in Fl. Cauc. Crit. III, 3, p. 207, p.p. (1903) : Moss, Cambr. Brit. Fl. III, p. 154 (1920) : Lemée, Dict. Gen. Phan. II, p. 887 (1930) : E. R. Saunders, Floral Morph. I, p. 40 (1937). *Aceranthus* Morr. & Dene in Ann. Sci. Nat. Bot., ser. 2, II, p. 349 (1834) : Endl. op. cit., no. 4813 (1839) : Spach, loc. cit. p. 61 (1839) : Benth. & Hook. f. op. cit. p. 44 (1862). *Vindicta* Rafin.

Fl. Tellur. II, p. 52, no. 187 (1837). *Endoplectris* Rafin. Fl. Tellur. III, p. 56, no. 636 (1837). *Epimedium* [sect. vel subgen.] *Eucpimedum* Franch. in Bull. Soc. Bot. France, XXXIII, p. 41 (1886) : Prantl in Engl. & Prantl, op. cit. p. 76 (1888) : N. Busch, loc. cit. p. 208 (1903) : Komarov in Acta Hort. Petrop. XXIX, p. 128 (1908) : Himmelbaur in Denkschr. Akad. Wiss. Math.-Nat. Wien, LXXXIX, p. 744 (1914). \times *Bonstedtia* † Wehrhahn, Gartenstauden, I, p. 455 (1930) : Wehrhahn in Bonstedt, Pareys Blumeng. I, p. 621 (1931) : Silva Tarouca & Schneider, Unsere Freiland-Stauden, ed. 5, pp. 99, 476 (1934).

The type-species of the genus *Epimedium* is *E. alpinum* Linn., based on Dodoens' *Epimedium*, not on Dioscorides'. The type-species of *Aceranthus* is *A. diphylloides* (Lodd.) Morr. & Dene ; that of *Vindicta* is *V. begonifolia* Rafin., likewise based on *Epimedium diphylum* Lodd. ; that of *Endoplectris* is *E. tricolor* Rafin., based on *Epimedium macranthum* Morr. & Dene. \times *Bonstedtia* Wehrhahn is a hybrid group, comprising the hybrids between *Epimedium* as represented by *E. macranthum* and *Aceranthus* as represented by *E. diphylum* ; \times *B. Youngiana* (Fisch. & Mey.) Wehrhahn, synonymous with *Epimedium Youngianum* Fisch. & Mey., sensu stricto, may be taken as the standard representative.

Flores dimeri : *sepala* *interiora*, *petala*, *stamina* 4.—*Herbae* *perennes*, *pilis* *multicellularibus* *instructae*. *Rhizoma* *repens*. *Folia* *omnia* *basalia* (sect. *Rhizophyllum*) *vel* *basalia* *et* *caulina* (sect. *Phyllocaulon*), *composita*, *foliolis* *ad* *marginem* *plerumque* *spinoso-dentatis* *raro* *integrис*. *Caulis* *florifer* *aphyllus* *vel* *foliatus* ; *inflorescentia* *simplex* *vel* *paniculata*, *pauci-* *vel* *multiflora*. *Flores* *varie* *colorati*. *Sepala* *exteriora* 4, *bracteiformia*, *mox* *decidua*. *Sepala* *interiora* *plerumque* *patentia*, *petaloidea*. *Petala* *plerumque* *calcarata* *vel* *saccata*, *raro* *plana* (subsect. *Aceranthus*), *nectarifera*. *Stamina* *erecta* ; *antherae* *valvulis* 2 *sursum* *dehiscentes*. *Pistillum* 1, *stylo* *elongato* *tenui* ; *ovula* ∞ , *biserialia*. *Capsula* *bivalvis* ; *semina* *allantoidea*, *arillata*.—*Species cognitae* *inter* 20 *et* 27, *omnes* *gerontogaeac*, *in* *silvis* *dumetisque* *temperatis* *Europae* *australis*, *Africæ* *boreali-occidentalis*, *Asiae* (*imprimis* *Sinae*) *incolac*.

Perennial herbs. *Rhizome* sympodial, irregularly branched, horizontally creeping, furnished with brown membranous leaves. *Leaves* basal or caudine, biannual, or rarely many times ternately divided (e.g. *E. elatum*), imparipinnate, trifoliolate, bifoliolate (e.g. *E. diphylum*), or abnormally unifoliolate ; *stipules* dimorphic, those of basal leaves expanded and united in front of the petiole into a membranous ligulate sheath to 1·5 cm. long, 1·3 cm. broad, those of caudine leaves distinct, oblong, inconspicuous, scarcely 2 mm. long, 1 mm. broad ; *petioles* terete but swollen and usually furnished with multicellular hairs at their junction and at insertion of leaflet ; *leaflets* glabrous above,

† Dedicated to Herr Carl Bonstedt (b. 1866), editor of 'Pareys Blumengärtnerei' etc., from 1900–31 Gartenoberinspektor in Göttingen.

frequently pubescent below, cordate at base, the lateral leaflets asymmetric, with the outer basal lobe longer than the inner, acute or acuminate at the tip, usually spiny at the margin but occasionally entire, involutely rolled before expansion. *Flowering stem* leafless or bearing 1 to 6 leaves; *inflorescence* simple or compound, with cymose lateral peduncles, few- or many-flowered, glabrous or glandular; *pedicels* subtended by and occasionally bearing a small membranous bract. *Flowers* dimerous, the terminal one occasionally pentamerous, regular, glabrous, white, rose, yellow, crimson, or violet, with imbricate aestivation; parts free, opposite. *Outer sepals* ('*sepala*' Morr. & Dene) 4, unequal, inner pair larger than the outer pair and up to 0.5 cm. long, usually scarious and quickly falling. *Inner sepals* ('*petala*' Morr. & Dene)

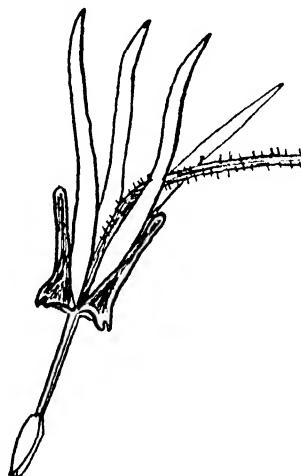


FIG. 14.—A flower of *Epimedium Fargesii*, $\times 2\frac{1}{2}$.

4, petaloid, spreading horizontally or rarely reflexing at anthesis. *Petals* ('*nectaria*' Morr. & Dene) 4, flat and petaloid or saccate and produced outwards into nectariferous pouches or spurs shorter or longer than the sepals. *Stamens* 4, connivent and appressed to the ovary but free from one another; *filaments* glabrous, without appendages; *anthers* dehiscing by two oblong valves which separate from the connective along their base and sides but remain attached at the top, curling upwards; *pollen grains* elliptic, smooth, with three longitudinal furrows, c. 25–40 μ long. *Ovary* superior, glabrous †, with parietal placentation; *ovules* several, in two series, anatropous, almost horizontal; *style* slender, with slightly dilated *stigma*. *Capsule* splitting to the

† Described, however, in *E. setosum* as being 'minutely puberulous,' see p. 489.

base as two independently veined valves, the larger and dorsal valve bearing the seeds and persistent style. Seeds smooth, almost black, rounded at both ends, allantoid, about 4 mm. long, with conspicuous aril.

Distribution.—South EUROPE, north AFRICA, ASIA Minor, Caucasus, India, China, Manchuria, Far Eastern Russia, Korea, Japan.

Features unusual in the genus and thus aids to determination are:—the very slender long *rhizomes* of *E. leptorrhizum*, *E. sutchuenense*; the 2-foliolate leaves of *E. diphyllum*; the suborbicular and coriaceous leaflets of *E. platypetalum*; the appressed bristle-like hairs on the lower side of leaflets in *E. sagittatum*, *E. acuminatum*; the leafless flowering stem of sect. *Rhizophyllum*; the numerous *stem-leaves* and leaflets of *E. elatum*, its tall growth and diffuse inflorescence; the minute inner sepals of *E. platypetalum*; the conspicuous yellow inner sepals of sect. *Rhizophyllum*; the spurless petals of subsect. *Aceranthus*; the 1 cm. long stamens of *E. Fargesii*, in other species c. 5 mm. long.

CLAVIS SPECIERUM SECTIONUMQUE EPIMEDII †.

- 1 a. Caulis florifer aphyllus. Sepala interiora conspicua, lutea, obovata, elliptica vel late ovata, \pm 1 cm. longa; petala parva, lumenis reductis, calcaribus brevibus, sepalis multo breviora; stamina exserta, \pm 5 mm. longa, filamentis \pm 3 mm. longis. (Sect. *RHIZOPHYLLUM*, p. 462.)
- 2 a. Folia 3-foliolata, pinnata vel biternata, foliolis 3, 5, 9 vel interdum numerosioribus margine plorunque sparse spinosis vel etiam integris. Transcaucasia, Persia.
- 3 a. Folia plorunque biternata. Sepala interiora late obovata; petala brevissima, vix 2 mm. longa, calcari brunneo
- 3 b. Folia plorunque 5- vel 3-foliolata, foliolis quam in a praecedente majoribus margine intordum integris. Sepala interiora late ovata vel elliptica: petala quam in a praecedente longiora, usque ad 4 mm. longa.
- 4 a. Sepala interiora flava; petala calcari brunneo recto vel paullum curvato sepali interioris tertiam partem aequante; antherae flavae, filamentis fore aequilongae.
- 4 b. Sepala interiora aurea; petala calcari aureo circinato-subrevoluta sepali interioris quartam partem aequante; antherae virides, filamentis breviores
- 2 b. Folia tantum 3-foliolata, haud pinnata vel biternata, foliolis 3 raro 1 rigidioribus margine undulatis spinosissimis. Calcar petali breve arcuatum. Algeria
- 1 b. Caulis florifer foliatus. (Sect. *PHYLLOCAULON*.)
- 5 a. Caulis florifer normaliter monophyllus, foliolis pluribus vel duobus.
- 6 a. Calcar petali aut nullum aut obtusum, usque ad 6 mm. longum, sepalo interiore brevius. Flores mediocres vel parvi, \pm 1-2 cm. diam.

[α *originarium*.]

1. *E. pinnatum*

[β *colchicum*.]

E. pinnatum

[γ *circinatum*.]

E. pinnatum

2. *E. Perrallerianum*.

† See also the key to cultivated species and hybrids (pp. 441-443).

7 a. Calcar nullum : petala plana obovata ; stamina inclusa, petalis multo breviora. Folia plerumque paucifoliolata. Herbae humiles, floribus campanulatis albis (? raro pallide roseis). Asia orientalis. (Subsect. ACERANTHUS.)

8 a. Folia saepe binata ; foliola ovata vel ovato-deltoides, basi saepe valde inaequilateralia, demum papyracea. Pedicelli glabri vel subglabri. Sepala interiora anguste ovata, \pm 6 mm. longa. Japonia.

9 a. Folia fere semper 2-foliolata ; foliola margine integra vel sparse spinosa. Inflorescentia simplex. Ovarium glabrum

9 b. 'Folia radicalia palmatim bidentata caulinata bifoliolata vel bi-binata ; foliola margine setosa Inflorescentia anguste paniculata, raro racemus simplex ovario minuto puberulo' (fide Koidzumi)

8 b. Folia 3- vel 5-foliolata (imparipinnata) ; foliola late ovata, fere orbicularia, basi (etiam foliolorum laterali) subaequilateralia, margine spinosissima, demum coriacea. Pedicelli valde pilosi. Sepala minuta. China

7 b. Calcar petali cylindricum, calceolatum, obtusum, usque ad 6 mm. longum, lamina petaloidea nulla, sepalo interiori anguste oblongo-ovato brevius ; stamina oxserta. Folia plerumque 9-foliolata, interdum 5-foliolata. (Subsect. MONOPHYLLON series MICRO-CERAE.)

10 a. Rhizoma tenuis, longissime repens. Foliola membranacea, plerumque autumno decidentia. Inflorescentia folio caulinio brevior. Sepala interiora atro-rubra

10 b. Rhizoma crassum, breviter repens. Foliola subcoriacea, per hiemem persistentia. Inflorescentia folium caulinum superans. Sepala interiora ochroleuca vel roseo-tincta

6 b. Calcar petali elongatum, subulatum, usque ad 2.5 cm. longum, plerumque sepalo interiori longius. Flores maximi, 3-5 cm. diam.

11 a. Folia bidentata vel triternata, foliolis 9-27. Calcar petali basi in laminam amplam expansum. Japonia, Korea. (Subsect. MONOPHYLLON, series MACROCERAE.)

24 a. Foliola papyracea, autumno decidentia. Flores vario colore :—petalis in vivo albis (f. α *normale*) vel violaceis (f. γ *violetaceum*) vel roseis (f. δ 'Rose-Queen') vel sulphureis (f. β *flavescens*)

24 b. Foliola subcoriacea, per hiemem viridia persistentia. Flores omnino albi

11 b. Folia plerumque tantum 3-foliolata, foliolis 3 raro 7.

25 a. Foliola late ovata vel fere orbicularia, obtusa. Sepala interiora oblongo-ovata, 20 mm. longa, 8-11 mm. lata. Calcar petali sepalum interius

7. *E. diphyllum*.

8. *E. setosum*.

9. *E. platypetalum*.

3. *E. alpinum*.

4. *E. pubigerum*.

5. *E. grandiflorum*.

5 bis. *E. sempervirens*.

subaequans, basi in laminam amplam expansum.
Rossia extremo-orientalis 6. *E. macrosepalum*.

25 b. Foliola anguste ovata vel ovata, longa acuminata.
 Sepala interiora anguste elliptica vel lanceolata,
 11–16 mm. longa, 4–5 mm. lata. Calcar petali sepalō
 interiore brevius, basi sine lamina. China 15. *E. leptorrhizum*.

5 b. Caulis florifer diphyllus, foliis oppositis vel raro alternis,
 vel raro triphyllus, foliolis plerumque 3 coriaceis. (Subsect.
 DIPHYLLON.)

12 a. Flores magni vel mediocres; calcar petali subulatum,
 elongatum, usque ad 2·5 cm. longum, sepalo interiore
 longius. (Series DOLICHOCERAE.)

13 a. Calcar caudiforme: petalorum laminae ampliae in
 formam poculi c. 0·8–1·3 cm. alti dispositae.

14 a. Folia 5- vel 3-foliolata, foliolis maturis ovatis vel
 late ovatis quam 6 cm. longitudine et 4·5 cm.
 latitudine plerumque minoribus. Folia radicalia
 caule florifero multo breviora. Pedicelli glandu-
 losissimi. Flores c. 2·3 cm. diam., calcaribus
 gracilibus subulatis. Szechwan 10. *E. Davidi*.

14 b. Folia (? semper) 3-foliolata, foliolis maturis angusto
 ovatis acuminatis c. 10–13 cm. longis et 6 cm. latis.
 Folia radicalia cauli florifero fere aquilonga.
 Pedicelli glabri. Flores ± 3·5 cm. diam., calcaribus
 crassioribus obtusis fere cylindricis. Hunan..... 11. *E. hunanense*.

13 b. Calcar cornutum; lamina petali aut nulla aut obso-
 lescentia.

15 a. Folia tantum 3-foliolata, foliolis coriaceis saepe
 longe acuminatis.

16 a. Foliola subter pilis appressis brevistrigillosa,
 interdum glabra, anguste ovata vel lanceolata.
 Inflorescentia plerumque glabra, raro pilis sparsis
 glandulosa, composita. Sepala interiora ± 1 cm.
 longa..... 12. *E. acuminatum*.

16 b. Foliola subter non brevistrigillosa sed pilis laxis
 gracilibus multicellularibus patentibus vel
 crispis sparse vel dense pubescentia. Inflores-
 centia glandulosa.

17 a. Sepala interiora acuta, vix 1 cm. longa.
 Rhizoma 2–5 cm. crassum.

18 a. Foliola plerumque ovata. Inflorescentia
 composita

18 b. Foliola plerumque angusto ovata. Inflores-
 centia simplex

17 b. Sepala interiora acuta vel acuminata, ± 1–
 1·7 cm. longa. Rhizoma ± 1–3 mm. crassum,
 valde elongatum, tenuissimum. Inflorescentia
 simplex, pauci- (4–8) flora.

19 a. Folia caulina duo aequaliter evoluta. Foliola
 subter sparse pubescentia pilis griseis vel
 subglabra. Sepala interiora longe acuminata.
 Szechwan, Hupeh

[α genuinum.] 13. *E. membranaceum*
 [β orientale.]
E. membranaceum

14. *E. sutchuenense*.

19 b. Folia caulina inaequaliter evoluta, alterum valde evolutum, alterum aut parvum abortivum aut nullum. Foliola subter in venis primariis et insertione potioli pilis rubris spissae pubescentia. Sepala interiora acuta vel breviter acuminata. Kweichow

15 b. Folia plerumque 9-foliolata, foliolis papyraceis acutis late ovatis. Flores flavi, \pm 2–3 cm. diam.; sepala interiora lanceolata, 4 mm. longa

12 b. Flores medios vel parvi: calcar petali obtusum, breve, usque ad 7 mm. longum, sepalum interiore brevius: stamina exserta. (Series BRACHYCERAE.)

20 a. Folia caulina plerumque biternata, interdum 5-vel raro 3-foliolata, foliolis ovatis vel late ovatis mox glabris. Sepala interiora anguste lanceolata, \pm 9 mm. longa, 3 mm. lata; calcar petali \pm 3 mm. longum: stamina \pm 4 mm. longa

20 b. Folia caulina tantum 3-foliolata.

21 a. Sepala interiora \pm 1.5 cm. longa, anguste lanceolata, acuminata, mox reflexa; calcar petali \pm 7 mm. longum, rectum (? atroviolaceum): stamina \pm 1 cm. longa. Inflorescentia saepius simplex, pauciflora (floribus 8–15)

21 b. Sepala interiora usque ad 7 mm. longa; calcar petali c. 2–4 mm. longum, saccatum; stamina \pm 5 mm. longa. Inflorescentia paniculata, multiflora (floribus 20–95).

22 a. Foliola subter pilis gracilibus mollibus patentibus vel crispis dense (praecipue f. *lanatum*) vel sparso (β *Cavaleriei*) pubescentia. Sepala exteriora ('bractae florum') minuta, vix 3 mm. longa; sepala interiora \pm 5–7 mm. longa, lanceolata vel anguste lanceolata, sepalis exterioribus et staminibus multo longiora

22 b. Foliola subter glabra vel pilis appressis brevistrigillosa. Sepala interiora majora, \pm 3.5–4.5 mm. longa; sepala interiora \pm 4 mm. longa, sepalis exterioribus et staminibus paulo breviora. Inflorescentia stricta (α *typicum*) vel diffusa (β *pyramdale*)

5 c. Caulis florifer polyphyllus, foliis (1–8) plerumque alternis, foliolis pluribus papyraceis ovatis vel suborbiculatis. Flores medios vel parvi. (Subsect. POLYPHYLLON.)

23 a. Folia plerumque biternata. Inflorescentia angusta, saepe simplex. Flores medios, \pm 2–3 cm. diam., calcaribus subulatis elongatis \pm 1–3 cm. longis. China occidentalis. (Series ELONGATAE.)

23 b. Folia pluri- (etiam 40-) foliolata. Inflorescentia diffusa, paniculata, saepe ramosa. Flores parvi, vix 1 cm. diam., calcaribus saccatis brevibus c. 3 mm. longis. Planta elata, foliacea. Himalaya. (Series ELATAE.)

15. *E. leptorrhizum*.

20. *E. elongatum*.

16. *E. brevicornu*.

17. *E. Fargesii*.

18. *E. pubescens*.

19. *E. sagittatum*.

20. *E. elongatum*.

21. *E. electum*.

ENUMERATIO EPIMEDII SPECIERUM.

SECTIO I. RHIZOPHYLLUM.

Epimedium sect. *Rhizophyllum* Fisch. & Mey., Sert. Petrop. I, sub t. 1 (1846).
Epimedium sect. *Dimorphophyllum* † Baill. Adansonia, II, p. 270 (1862); Hist. Pl. III, pp. 55–6, in adnot. (1871); Nat. Hist. Pl. III, pp. 56–7, in adnot. (1874).
Epimedium [subgen.] *Euepimedium* [sect.] *Gymnocaulon* Franch. in Bull. Soc. Bot. France, XXXIII, p. 40 (1886): N. Busch in Fl. Cauc. Crit. III, 3, p. 208 (1903): Komarov in Acta Hort. Petrop. XXIX, p. 128 (1908).

'Nectaria brevia, depressa, cucullata; lamina nulla. Folia omnia radicalia. Scapus aphyllus. Petala flava' (Fisch. & Mey.).

Rhizome elongated. *Leaves* normally all basal, with subcordiaceous ± ovate *leaflets*. *Inflorescence* simple. *Inner sepals* yellow, rounded at tip, obovate, elliptic or ovate, up to 1 cm. long, 8 mm. broad. *Petals* reduced to small nectaries with blunt nectariferous projections or spurs up to 3 mm. long and yellow usually dentate laminae up to 3 mm. deep, 3 mm. across. *Stamens* protruding, about 5 mm. long, with filaments equalling or exceeding anthers.

This well-defined section is easily recognized by its leafless flower-stalk, yellow flowers, very small petals, and protruding stamens. It inhabits western Asia and north Africa.

Type-species:—*E. pinnatum* Fisch.

1. EPIMEDIUM PINNATUM Fischer, sensu lato.

E. pinnatum Fischer (!) in DC. Veg. Syst. II, p. 29 (1821): Boiss., Fl. Or. I, p. 102 (1867): Franch. in Bull. Soc. Bot. France, XXXIII, p. 104 (1886): Voss, Vilmorin's Blumeng., I, p. 51 (1894): N. Busch in Fl. Cauc. Crit. III, 3, p. 208 (1903): Wehrhahn, Gartenstauden, I, p. 453 (1930).

This collective species inhabits the east and west Caucasus and north Persia; it is absent from the central Caucasus: the distribution thus corresponds to that of other Tertiary plants in the Caucasus which from being spread over the whole have retreated into the widely separated maritime districts of Lenkoran and Pontus-Colchis; cf. Kusnezow (1909) or Palibin in Bull. Soc. Bot. Genève, 2e ser., II, pp. 22–24 (1910). Three subspecies, with claims to specific rank, may be distinguished:—

Subsp. α ORIGINARIUM Stearn, nom. nov.

E. pinnatum Fisch. (!) in DC., loc. cit. (1821): C. A. Meyer, Verz. Pflanz. Cauc. Casp. p. 175 (1831): Fisch. & Mey., Sert. Petrop. I, t. 1* (1846): Boiss. loc. cit., p.p. et excl. β (1867); Franch., loc. cit., p.p. et excl. β (1886); N. Busch, loc. cit., excl. β (1903): Komarov in Acta Hort. Petrop. XXIX, p. 129 (1908): Grossheim in Beih. Bot. Centralbl., XLIII, 2, p. 19 (1927); Grossheim, Fl.

† δι-μορφος, two-formed; φύλλων, leaf; apparently in allusion to the outer and inner sepals (*phyllo* in old terminology) being of very different form.

Kavkaza, II, p. 124 (1930), sensu stricto. '*E. pieroceras* Morr.', secundum Baker (!) in Gard. Chron., n.s. XIII, p. 683 (1880), vix vel non Morr. *E. Sieboldianum* G. Koidzumi (!) in Bot. Mag. Tokyo, XLIV, p. 95 (1930); Nemoto, Fl. Jap. Suppl. p. 236 (1936).

Figures.—Fisch. & Mey., Sert. Petrop., t. 1*: Gardening Illustr. LIV, p. 31 (Jan. 1932), flos.

Plant in flower 20–30 cm. high. *Rhizome* long-creeping, somewhat nodose, 3–4 mm. thick. *Leaves* all basal, often biennial (9 leaflets), less often pinnate (5 or 11 leaflets) or trifoliolate, covered when young with long white or reddish hairs, later nearly glabrous; *leaflets* narrowly ovate to broadly ovate, the tip acute, the margin spinous-serrate, the base deeply cordate with usually rounded lobes, at length subcoriaceous, dark green above, glaucescent beneath, small at flowering time but later up to 8 cm. long, 7 cm. broad. *Flowering stem* leafless, equalling the leaves, ending in a simple loose glandular or glabrous *raceme* of 12–30 flowers; *pedicels* 1–1.5 cm. long. *Flowers* about 1.6 cm. across. *Outer sepals* ('flower-bracts') oblong-ovate, blunt, brownish with hyaline margin, about 3–5 mm. long, 1–2 mm. broad. *Inner sepals* broadly obovate, rounded, yellow, sometimes streaked with red near the short basal claw, about 8 mm. long, 6 mm. broad. *Petals* very small, scarcely 2 mm. in total length, with dentate reduced yellow laminae 1–2 mm. deep and 3 mm. across and brownish-purple nectariferous projections or spurs scarcely 1 mm. long. *Stamens* protruding, 5 mm. long; *anthers* yellow, 2–2.5 mm. long.

Distribution.—North PERSIA (prov. Gilan) and the adjoining Talysh district (Lenkoranskii yezd) of eastern TRANSCAUCASIA near the Caspian Sea, in mountain woods.

Although long known, this plant is poorly represented in herbaria; there are few specimens and these mostly lack flowers. De Candolle described it from a tracing of a specimen in Pallas' herbarium which was sent to him by F. E. L. Fischer; this drawing, now in the Prodromus herbarium of the Conservatoire de Botanique at Geneva, bears Fischer's note: '*Epimedium pinnatum* m. in prov. Persiae Gilan lecta a cl. Hablizl. Hb. Pallasii'. C. A. Meyer introduced it into cultivation, probably in 1830, and, from a living plant grown at Petrograd, he and Fischer published a detailed description and coloured plate (Sert. Petrop. t. 1). Since then this original Caspian plant has been almost lost sight of, the '*E. pinnatum*' of later authors being mostly the western Colchic subspecies.

Type-locality.—'Persia provincia Gilan' (DC., loc. cit.).

PERSIA :—Prov. Gilan: without exact locality, *Hablizl* (Gen. ! icon. authent.) *Gmelin Jr.* (Calcutta !); in the Talysh range of mountains, below Massula, wooded spurs near Lengerud, *Buhse* 931 (Boiss. ! V ! Zürich !). Langarud (Lengerud) and Masuleh (Massula) are about 55 km. west of Resht.

AZERBAIJAN, U.S.S.R. :—Talysch district : in very shady woods of Talüscher between Lenkoran and Suwant, alt. 400 m., Meyer (L. ! cf. C. A. M., loc. cit. ; 1831) ; Suwant, Hohenacker 2763 (L. !) ; between the frontier post Sardoli and the village of Unus, on a shady damp slope in thick woodland, Shipczinsky 1174 (L. !).

This is the eastern and ‘typical’ subspecies of *E. pinnatum*, sensu lato, distinguished by its often binate leaves, slightly obovate inner sepals, and minute-spurred petals. Grossheim (1927) includes it in his group of ‘autochthonous Hyrcanian species, relics of an eastern Old-Mediterranean centre which extended throughout the Pontic region, the Caucasus and the southern Caspian provinces, the Hyrcania of the Ancients’.

Koidzumi’s *E. Sieboldianum* was described as a new Japanese species from a specimen (Rijks Herb., Leiden, sheet no. 898, 196–202 !) bearing the printed label ‘Herb. Lugd. Batav. Japonia’ and determined by Miquel as ‘*Aceranthus sagittatus* Sieb. & Zucc. var.’, a later hand adding the name ‘Siebold’ as collector. This is the only evidence of its supposed Japanese origin ; there is no label in Siebold’s own hand-writing as is found on many specimens of undoubtedly Japanese origin at the Leiden herbarium. I cannot distinguish it in any way from the Caspian *E. pinnatum* and think that it is a cultivated specimen of this species, probably grown in Siebold’s nursery at Leiden and by accident labelled as coming from Japan, whence Siebold had introduced so many plants (cf. Stearn in Gard. Chron. ser. 3, xcii, p. 347 ; 1932). If truly a native of Japan it is remarkable that so distinct a plant should be known only from one old specimen in a European herbarium ; there are no east Asiatic species resembling it.

Subsp. β COLCHICUM † Boissier.

? *E. colchicum* hort. ex Maund, Bot. Gard. XII, t. 276, no. 1102 *, sine descript. (1848). ‘*E. pinnatum* Fisch.’, sec. Morr. in Ann. Soc. Agric. Bot. Gand. II, p. 139, t. 61* (1846) : Hook. in Bot. Mag. LXXV, t. 4456* (1849) ; auct. anon. in Ann. of Hort. v, 377, cum icono (1850) : Morr. in Belgique Hort. IV. p. 35, t. 6* (1854) ; Boiss. loc. cit., p.p. (1867) : Baker, loc. cit., p.p. (1880) ; Franch. loc. cit., p.p. (1886) : Alboff, Prod. Fl. Colch. p. 15 (1895) ; Komarov, loc. cit., p.p. (1908),—non Fisch., sensu stricto. *E. pinnatum* var. *colchicum* Boiss. (!), loc. cit. (1867) : Franchet, loc. cit. p. 104 (1886) : Woronow in Sched. Herb. Fl. Ross. no. 1704 (1908). *E. colchicum* hort. ex Ann. of Hort. loc. cit. (1850), ex Morr. loc. cit. (1854), ex Boiss. (!), loc. cit. (1867), omnes pro syn. ‘*E. pinnati*’ ; Vilmorin-Andrieux, Fleurs Pleine Terre, p. 226 (1863) ; ed. 2, p. 297 (1866) ; ed. 3, p. 375 (1870) : ‘Fischer mss.’ ex Baker, loc. cit. pro var. (1880) : Cosson, Illust. Fl. Atlant. I, p. 9 (1882), et Compend. Fl. Atlant. II, p. 57 (1887), in obs. : Trautvetter, Inserm. Fl. Ross. I, no. 274 in Acta Hort.

† ‘*colchicum*’ :—from Colchis (*Kολχίς* of Strabo), in ancient Greek geography the almost triangular district of west Transcaucasia (Georgia) at the south-east corner of the Black Sea (Pontus Euxinus) now represented by Abkhazia.

Petrop. VIII, p. 65 (1883) : Komarov, loc. cit. (1908) : Sosnovsky in Monit. Jard. Bot. Tiflis, N.S. I, p. 75 (1923) ; Bergmans, Vaste Pl. p. 202 (1924) ; Grossheim, Fl. Kavkaza, II, p. 124 (1930). '*E. macranthum*' The Garden, XLVI, p. 356 in icones *, '*E. pinnatum*' Goldring in textu (1894) ; *E. pinnatum* var. *integri-folium* Medwedow & Alboff (!) ex Alboff, loc. cit. † (1895). *E. pinnatum* f. *colchicum* Voss, loc. cit. (1894). *E. pinnatum* subsp. *colchicum* (Boiss.), cum f. *integrifolio* (Alboff), N. Busch, loc. cit. p. 209 (1903). *E. pinnatum elegans* hort. (!) ex W. Miller in Bailey, Cycl. Am. Hort. II, p. 536 (1900) ; Silva Tarouca, Unsere Freiland-Stauden, p. 93 (1910) ; ed. 2, p. 168 (1913) ; ed. 3, I, p. 191 (1922) ; Farrer, Engl. Rock-Gard. I, p. 327 (1919) ; Bergmans, Vaste Pl. p. 203, fig. 46 (1924). *E. elegans* hort. ex Bergmans, loc. cit., pro syn. (1924).

Figures.—Bot. Mag. t. 4456* ; Ann. Soc. Agric. Bot. Gand. II, t. 61* ; Belg. Hort. IV, t. 6* ; Ann. of Hort. V, p. 377 ; The Garden, XLVI, p. 356*.

Plant in flower 25–40 cm. high. *Rhizome* long-creeping, about 5 mm. thick. *Leaves* all basal, usually 3- or 5-foliolate ; *leaflets* ovate to broadly ovate, the tip acute, the margin sparsely spinous-serrate or even entire (*forma integrifolium* Alboff), the base deeply cordate with rounded frequently overlapping lobes, dark green above, glaucous beneath, frequently evergreen, up to 15 cm. long, 11 cm. broad. *Flowering stem* leafless, ending in a loose glandular or glabrous *raceme* of 15–20 (or more) flowers. *Flowers* about 1·8 cm. across. *Outer sepals* oblong-ovate, blunt, 3–5 mm. long, 1–2 mm. broad. *Inner sepals* rounded, aureolin-yellow, the outer pair broadly ovate about 7 mm. broad, the inner pair almost elliptic ('oblong') and slightly narrower. *Petals* small, up to 3·5 mm. in total length, with dentate reduced yellow laminae about 2 mm. deep and straight or slightly upcurved, brown or yellow (*forma concolor* C. Morr. in Belg. Hort. IV, p. 35, pro var. ; 1854), spurs about 2 mm. long. *Stamens* protruding, 5–6 mm. long ; *anthers* yellow, 2·5–3 mm. long.

Distribution.—Western TRANSCAUCASIA, in moist mountain woods † between 500–4000 ft. on the south-west side of the main Caucasian mountain chain, having been often collected in Abkhazia (e.g. near the river Mzymty, Gagry, Pitsunda, Psyrtskha or Novo Afon, Tsebeldinsk, and Sukhum ; cf. Busch, loc. cit.), but rarely in Mingrelia (found by Alboff near Mukhuri) and Adzharia (Adjaria or Batumskaya oblast). Its most northern station seems to be near Vardane (about 10 miles north of Sochi) in the Chernomorskaya government of the North Caucasus, its most southern in north-east Asia Minor (Lazistan, 'à l'embouchure du Kalo-potames, Juin 1866', *Balansa*, ? from near Khala) ;

† 'Foliis integerrimis saepius majoribus. Abhasia : m. Mamdzishkha 1300–1350 m. (N.A. 1894). Mingrelia ; vallis fl. Khopsis-tzkali prope Mukhuri 800 m. (N.A. 1893). Adzharia : vallis fl. Merissi prope Kedy (Medwedow 1886 ; N.A. 1893, nos. 164, 168–175)' (Alboff, loc. cit.). Boiss. !

‡ The Tertiary composition of these Caucasian woods and the resemblance of the humid but temperate climate here to that of Japan may be noted ; cf. N. Alboff : 'Les forêts de la Transcaucاسie occidentale' in Bull. Herb. Boissier, IV, pp. 60–77 (1896).

Mr. E. K. Balls in 1933 saw an *Epimedium* (distinct from *E. pubigerum*), growing with *Iris unguicularis* on burnt-over scrub-covered hillsides above Surmene ($40^{\circ} 55' N.$, $40^{\circ} 4' E.$), which was probably *E. pinnatum* β *colchicum*, but his material went astray in the Turkish post. The following exsiccata are in many herbaria :—

GEORGIA, U.S.S.R. :—Abkhasia : Suchum Kale, *Busch*, *Marcowicz*, & *Woronow*, Fl. Caucas. Exsicc. 108 (B.' etc.) ; in woodland by the river Psyrtscha, *Gubbis* in *Grossheim* & *Schischkin*, Pl. Orient. Exsicc. 1928, no. 385 (B.M. !) ; prov. Suchum in woods at Jurjewskoje (near Suchum), 27. iii. 1903, fl., 13. iv. 1903, fr., *Woronow* in Herb. Fl. Ross. 1704 (B. ! etc.). Adzharia : pass of Merissi near Kedy, *Alboff*, Pl. Adjarie 1893, no. 175, as var. *integrifolium* (Boiss. ! B. ! etc.).

This western subspecies diverges from *E. pinnatum* α *originarium* chiefly in its longer petal-spurs, ovate inner sepals, and usually 3- or 5-foliolate leaves with larger and less spinous or even entire-margined leaflets. Concerning the latter, Woronow writes (in Russian), in Herb. Fl. Ross., no. 1704) :—‘ In many of the present specimens the edges of the leaflet are entirely without spines or have only one or two pairs on the lower part. Medwedow and Alboff distinguished these as a special variety *integrifolium*. In Transcaucasian forests I often found both entire and spiny leaflets on one and the same leaf. This characteristic is purely individual and Alboff’s variety cannot be maintained’. The plant cultivated has apparently broader inner sepals than wild specimens. It is known in gardens as *E. colchicum*, ‘*E. pinnatum*’, and *E. pinnatum elegans*, the spines of bright yellow *Verbascum*-like flowers being very ornamental in April and the foot-high leaves remaining green all winter ; it grows vigorously under almost any conditions. According to Morren (1846) and Fischer, in a letter quoted by Hooker (Lond. Journ. Bot. 1, p. 207 ; 1842) and by Lindley (Bot. Reg. XXXII, sub t. 9 ; 1846), all of whom refer to it as ‘*E. pinnatum*’, this plant was sent from Abkhasia by Count Worontzoff to N. de Hartwiss of the Nikita Botanic Garden, who introduced it into European gardens about 1842, apparently under the provisional name *E. colchicum*. This name has been continuously used in gardens to the present day ; but its first valid publication is uncertain, as botanists for a long time regarded the plant as identical with ‘typical’ *E. pinnatum* from the Caspian and mentioned *E. colchicum* only as a horticultural synonym. Consequently most of the figures and literature on ‘*E. pinnatum*’ really refer to β *colchicum*, a fact not appreciated by Franchet and Komarov, though they separate the two. Apparently Cosson was the first to regard them as distinct species.

Subsp. γ CIRCINATUM Stearn, nom. nov.

E. circinnato-cucullatum Sosnovsky in Monit. Jard. Bot. Tiflis, n. ser. 1, p. 75 (1923) ; Grossheim, Fl. Kavkaza, II, p. 124 (1930).

‘*Folia imparipinnatisecta*, 1–2-juga, vel biternatisecta, *segmentis* ovatis profunde cordatis breviter acuminatis, margine plus minus spinuloso-serratis.

Racemus simplex; petala aurea, appendice nectarifera aurea cucullata, petalo [sic] quadruplo breviore, in calcar breve circinnato-subrevolutum concolor abeunte. Staminum filimenta anthera 1½-plo longiora viridia. Perennis.

Hab. prope Sotshi. Plantam vivam vidi in sectione Colchica Horti Botanici Tiflisiensis cultam' (Sosnovsky, loc. cit.).

Examining the Epimediu*m*s grown in the Colchic section of the Tiflis Botanic Garden under the name *E. colchicum* and obtained from various parts of western Transcaucasia, D. Sosnovsky was able to distinguish three kinds, contrasting them as follows (translated from the Russian) :—

Locality whence obtained :—	(1) Dzhvari, Zugdidui, Novosonaki.	(2) Sochi.	(3) Tiflis Bot. Gard., mixed with others.
Sepal :—	sulphur yellow.	bright yellow.	bright yellow.
Petal :—	in its widened part sulphur-yellow, the spur brown, straight, $\frac{1}{2}$ the length of sepal.	entirely bright yellow, towards the tip convoluted like a snail-shell, $\frac{1}{2}$ the length of sepal.	in its widened part yellow, the spur brown, slightly up-curved, shorter than in first kind.
Stamen-filament :—	almost the same length as anther.	half as long again as anther.	as in first kind.
Anther :—	yellow.	green.	green.
Determined by Sosnovsky as :—	<i>E. colchicum</i> .	<i>E. circinnato-cucullatum</i> , sp. n. (ad interim).	probably hybrid between 1 and 2.

The first and second differed in definite floral characters, while the third, of which individuals grew scattered among patches of the others, had features belonging to one or the other of these and appeared to be a hybrid between them ; the vegetative organs were similar in all three. The second kind from Sochi with yellow curled petal-spurs and green anthers Sosnovsky provisionally described as a new species, *E. circinnato-cucullatum* ; I prefer to regard it as a subspecies of the collective *E. pinnatum*.

Sochi, the type-locality of *E. circinnato-cucullatum*, is near the Black Sea in the Chernomorskaya government of North Caucasus (Severnuii Kavkaz), U.S.S.R. (43° 35' N., 39° 40' E.), 163 miles north-west of Batum. According to Sosnovsky, specimens collected at Sochi by Medwedow (Medvedeff) belong to typical *E. colchicum*.

2. E. PERRALDERIANUM Cosson.

E. Perralerianum Cosson (!) in Bull. Soc. Bot. France, VIII, p. 607, nomen (1862); IX, p. 167, cum descript. (1862) : Baker in Gard. Chron. N.S. XIII,

p. 683 (1880) : Hook. f. in Bot. Mag. cvi, t. 6509* (1880) : Cosson, Illustr. Fl. Atlant. I, p. 9, t. 5 (1882), and Compend. Fl. Atlant. II, p. 57 (1887) : Franch. in Bull. Soc. Bot. France, xxxiii, p. 105 (1886) : Battandier, Fl. Algér. Dicot. p. 18 (1888) : Komarov in Acta Hort. Petrop. xxix, p. 130 (1908).

E. pinnatum var. *Perralderianum* (Cosson) Wehrhahn, Gartenstauden, I, p. 453 (1930), and in Bonstedt, Pareys Blumeng. I, p. 621 (1931) as 'var. *Peralderianum*'.

Figures.—Bot. Mag., t. 6509* ; Cosson, Illustr., t. 5.

Plant in flower 15–30 cm. high. Rhizome long-creeping, 2–4 mm. thick. Leaves all basal, trifoliolate or rarely unifoliolate, never pinnate or biernate; leaflets ovate to broadly ovate, the tip acute, the margin undulate, rigid and very spinous-serrate, the base deeply cordate with rounded subequal lobes, at length firm and subcoriaceous, often bronzed when young, glaucescent and ultimately subglabrous beneath, from 2·5 cm. long, 2 cm. broad, to 6·5 cm. long, 5·5 cm. broad, or under cultivation even to 10 cm. long, 7 cm. broad. Flowering stem leafless, equaling the leaves, ending in a simple very glandular raceme of 9–25 flowers; pedicels 1·2–2·5 cm. long. Flowers 1·5–2·3 cm. across. Outer sepals greenish, oblong-ovate, blunt, 4–5 mm. long, 1–2 mm. broad. Inner sepals obovate, rounded, aureolin-yellow, 8–11 mm. long, 5–9 mm. broad. Petals small, 2·5 mm. in total length, with dentate yellow laminae 2–3 mm. deep and brown upcurved spur 1–2 mm. long. Stamens protruding, 5 mm. long; anthers yellow, 2–2·5 mm. long.

Distribution.—NORTH AFRICA, ALGERIA, east Kabylia (approx. 36° 30' N., 5° 25' E.) growing at 3600 to 4500 ft. in the shade of oaks and cedars (*Cedrus atlantica*) on the Chaîne des Babors.

Type-locality.—‘In silvaticis umbrosis quercinis regionis montanae in provincia Cirtensis Kabylia orientali, ad 1200–1500 met., *Paeoniae Russi* † socia; in ditione Beni-Foughal ad fontem El-ma-Berd ! (*H. de la Perraudière*), in monte Tababor ! haud infrequens in monte Babor !’ (Cosson, loc. cit.; 1863).

The following authenticated exsiccata are in many herbaria :—

ALGERIA :—In shady woods of mount Tababor in east Kabylia, 1300–1500 m. alt., 1861, *Kralik*, Plant. Alger. Exsicc. 100 (K. ! P. ! etc.); Djebel Tababor †, prov. of Constantine, on the north slope in the shade of cedars, *Cosson & Reboud* in Soc. Dauphin. 1881, no. 2742 (K. ! etc.).

E. Perralderianum is closely allied to *E. pinnatum* β *colchicum*, but may be

† Non Bivona = *P. algeriensis* Chabert, syn. *P. corallina* var. *atlantica* Cosson.

‡ According to Trabut (in Bull. Soc. Bot. France, xxxvi, p. 61; 1889) the north slope of the Babor massif is ‘entièrement couvert par un forêt très boisé de Cèdres, *Abies numidica*, *Acer obtusatum* [var. *africanum* Pax], *Populus tremula*, *Quercus Mirbeckii* souvent couvert de galles, *Ilex Aquifolium*, *Taxus baccata* et *Quercus Afares*. . . . Deux raretés habitent sous la futaie du versant nord : l'*Epimedium Perralderianum* et le *Campanula trichocalycina*’—an essentially temperate flora. It is this region of Algeria ‘qui reçoit le maximum de pluies annuelles’. See also Elwes & Henry, Trees, iv, p. 738 (1909), and Barbey (1934).

readily distinguished by its trifoliolate (never pinnate or binate) leaves with firmer leaflets distinctly undulate and very spinous at the margin (the spines about twice as long as those of *E. pinnatum* β *colchicum* grown under the same conditions) as well as more evidently veined above. It is also of dwarfer habit and sufficiently distinct in distribution and in flower (the inner sepals being broadest at or above the middle, instead of below the middle as in *E. pinnatum* β *colchicum*, and the spur of the petal being bent upwards from the lamina at an angle of about 45° , instead of 90° as in *E. pinnatum* β *colchicum*) to be reckoned a good species. The name commemorates Henri René le Tourneux de la PERRAUDIÈRE (1831–61), an enthusiastic young French naturalist who collected with Bourgeau in the Canary Islands and died of fever while accompanying Cosson in north Africa. Cosson introduced the plant into European gardens and it was from cultivated material many years after its original publication that the flowers were first described.

SECTIO II. PHYLLOCAULON.

Epimedium [subgen.] *Euepimedium* [sect.] *Phyllocaulon* Franch. in Bull. Soc. Bot. France, XXXIII, p. 40 (1886); N. Busch in Fl. Cauç. Crit. III, 3, p. 209 (1903); Komarov in Acta Hort. Petrop. XXIX, p. 130 (1908).

‘Caulis floriferus foliatus, foliis 1 vel 2 vel pluribus’ (Franchet, loc. cit.). Flowering stem bearing one, two, or several leaves. This group occurs in Europe, Asia Minor, India, China, and Japan.

Standard species:—*E. alpinum* Linn.

Subsectio 1. MONOPHYLLON.

Epimedium subgen. *Euepimedium* sect. *Phyllocaulon* series *Monophylla* Komarov in Acta Hort. Petrop. XXIX, p. 130 (1908).

‘Caule florifero monophyllo, foliis ternatisectis’ (Komarov, loc. cit.). Flowering stem bearing one leaf. Leaves usually binate. Petals saccate or horn-shaped, not spurless and flat.

Standard species:—*E. alpinum* Linn.

Series *Microcerae*.

Epimedium Linn, Sp. Pl. p. 117 (1753); Gen. Pl. ed. 5, p. 53 (1754), sensu stricto. *Epimedium* sect. *Microceras*, excl. *E. elato*, Morr. & Dcne in Ann. Sci. Nat. Bot., ser. 2, II, p. 349 (1834): Spach, Hist. Veg. Phan. VIII, p. 57 (1834): Fisch. & Mey. Sert. Petrop. sub t. 1 (1846): Baill. Adansonia, II, p. 270 (1862): Hist. Pl. III, p. 56, in adnot. (1871). *Epimedium* subgen. *Microceras* Seringe, Fl. Jardins, III, p. 272 (1849).

Flowers 0·9–1·3 cm. across. Inner sepals narrowly ovate, concave. Petals shorter than the inner sepals, saccate and slipper-like, blunt, with no basal laminae. Stamens protruding.

This group occurs in south Europe and Asia Minor.

Standard species:—*E. alpinum* Linn.

3. E. ALPINUM Linnaeus.

Epimedium auct. ante-Linn. plur. (sed non Dioscorides) :—*Anguillaria*, Semplici, p. 253 (1561), reimpr. in Langkavel, Bot. Spaet. Griechen, p. 35 (1866) : *Calzolaria* [Calceolari], Viaggio di Monte Baldo, p. 10 (1566), fide Saccardo et Bertoloni : Pena & L'Obel, Stirp. Adversaria Nova, p. 138, cum iconе (1570) ; L'Obel, Pl. Stirp. Hist. p. 176, cum iconе (1576) ; Kruydtboeck, p. 399, cum iconе (1581) : Dodoens, Hist. Stirp. Pempt. Sex, p. 589, cum iconе (1583) ; ed. 2, p. 599 (1616) ; Calceolari, Iter Baldi [p. 5] in J. Camerarius, De Pl. Epit. . . . Matthioli (1586) : J. Camerarius, Hort. Medicus, p. 57 (1588) : *Tabernaemontanus*, Eicones, p. 774, cum iconе (1590) : Gerard, Herball, p. 389, cum iconе (1597) ; ed. Johnson, p. 480, cum iconе alter.† (1636) : L'Obel, Dilucid. Simpl. Med. Stirp. Advers. p. 138, cum iconе (1605) : Parkinson, Paradisi in Sole, p. 283 (1629) : Theatrum Bot. p. 1366, cum iconе (1640) : Bodaeus a Stapel, Theoph. Hist. Pl. p. 823, cum iconе (1644) : Morison, Pl. Hist. Univ. Oxon. I. p. 196 (1680) : Ray, Hist. Pl., II, 1330 (1688) : Tournefort, Inst. Rei Herb. p. 232, t. 117 (1700) : Salmon, Botanol. Engl. Herb. I, p. 64, cum iconе (1710) : [Martyn] Compl. Herbal of Tournefort, I, p. 475, t. 118 (1719) : Boerhaave, Hist. Pl. Lugd. Batav. I, p. 388 (1727) ; Index alt. Hort. Lugd. Batav. I, p. 307 (1727) : Lindern, Hort. Alsat. p. 137, t. vi (1747) : Linn. Hort. Cliff, p. 37 (1737) : Hort. Upsal. p. 29 (1748) : Wienmann & Bieler, Phytanthoza Icon. II, p. 389, t. 479, fig. b* (1739) : Miller, Gard. Dict. ed. 6 (1752) ; ed. 7 (1759) : Hill, Brit. Herbal, p. 228, t. 33 (1756). *Epimedium Dodonavi* [Dalechamps] Hist. Gen. Pl. 1095, cum iconе (1587) : Valentini, Viridarium Reform. t. 66 (1719). *Epimedium quorundam* J. Bauhin, Hist. Pl. Univ. II, p. 391, cum iconе (1651). *Epimedium Dioscoridis* [Marchant in] Recueil Pl. Louis XIV, t. 127 (c. 1788)‡. *E. alpinum* Linn. (!) Sp. Pl. p. 117 (1753), et auct. plur. : Kniphof, Herb. Viv., cent. X. t. sine no.* (1758) : Miller Gard. Diet. ed. 8 (1768) : Roemer, Fl. Europaea Inchoata, I, [t. 8]* (1797) : Sowerby & Smith, Engl. Bot. VII, t. 438* (1798) ; ed. 2, II, p. 13, t. 226* (1835) ; ed. 3, of Syme, I, t. 52* (1863) : Sibthorp & Smith, Fl. Graeca, II, p. 39, t. 150* quoad iconе, descript. et syn., sed loc. excl. (1813) : DC. Veg. Syst. II, p. 28, excl. var. β (1821) : Bertoloni, Fl. Ital., II, p. 192 (1835) : Reichenbach, Icon. Fl. Germ. III, t. 18, no. 4485* (1838–9) : Seringe, Fl. Jardins, III, p. 272 (1849) : Schlosser & Vukotinovic, Fl. Croat. p. 190 (1869) : Baker in Gard. Chron., N.S. XIII, p. 620, excl. var. (1880) : Schlechtendal, Langethal & Schenk, Fl. Deutschl., ed. 5, of Hallier, XII, p. 17* (1883) : Franch. in Bull. Soc. Bot. France, XXXIII, p. 106, excl. var. (1886) : Fiori & Paoletti, Icon. Fl. Ital. p. 188 (1895) : Fiori, Nuov. Fl. Analit. Ital. I, p. 691 (1924) :

† The woodcut of *E. alpinum* in Gerard (1597) is that of *Tabernaemontanus* (1590), the London printer Norton having procured the wood-blocks of the latter's work from Frankfurt-a-Main ; Johnson (1636) replaced this by L'Obel's less accurate cut which (with minor alterations) is also used by Dodoens, Dalechamps, Parkinson, Salmon, Hill, and others.

‡ These plates were prepared about 1675, but not published until about 1788.

Pampanini, *Essai Géog. Bot. Alpes*, 95, map vi. n. 85 (1903), in *Mém. Soc. Fribourg. Sci. Nat. ser. Géol.* III, fasc. 1; Pampanini, *Sched. Fl. Ital. Exsicc.*, no. 574, in *Nuov. Giorn. Bot. Ital. N.S.* xiv, p. 105 (1907); Hayek, *Fl. Steiermark*, I, p. 358 (1908); Komarov in *Acta Hort. Petrop.* xxix, p. 130, excl. syn. '*E. rubrum*' (1908); Bonnier, *Fl. Illustr. France, Suisse*, I, p. 43, t. 23, fig. 101* (1911); Hegi, *Illust. Fl. Mitt.-Europa*, IV, p. 9, fig. 721 (1913); Moss, *Cambridge Brit. Fl.* III, p. 155, t. 165 (1920); *E. alpinum* f. *normale* Voss, *Vilmorin's Blumeng.* I, p. 50 (1896).

Figures.—Kniphof*; Roemer*; Sowerby and Smith*; Sibthorp and Smith*; Reichenbach*; Le Maout and Decaisne, *Gen. Syst. Bot.* p. 203; Schlechtendal, Langethal and Schenk*; Fiori and Paoletti, *Icon.*; Bonnier*, Hegi; Moss; *vide supra*; others are enumerated in Staph, *Index Londin.*, III, p. 54 (1930).

Plant in flower 6 cm. (i.e. dwarfed alpine specimens) to 30 cm. high. *Rhizome* long-creeping, 2–4 mm. thick. *Leaves* basal and caudine, usually biennial, rarely trifoliolate; *leaflets* ovate, the tip acute or acuminate, the margin spinous, the base deeply or shallowly cordate, membranous in texture, bright green above, often marginally red-tinged when young, at first pubescent beneath but usually becoming subglabrous, variable in size but attaining 13 cm. long, 8.5 cm. broad, under cultivation. *Flowering stem* bearing one biennial leaf; *inflorescence* compound, loose, glandular, usually many- (8–26) flowered, nearly always slightly or much shorter than the stem-leaf; lower peduncles 2–3-flowered; *pedicels* usually 5–15 (sometimes up to 25) mm. long. *Flowers* 9–13 mm. across. *Outer sepals* grey, speckled red, oblong to obovate, 2.5–4 mm. long, 2 mm. broad. *Inner sepals* narrowly ovate, blunt or subacute, concave, dull garnet-red, 5–7 mm. long, 3 mm. broad. *Petals* slightly shorter than the inner sepals, slipper-like, cylindric, 4 mm. long, canary-yellow, with no basal laminae. *Stamens* protruding, 3 mm. long; *anthers* 2 mm. long. *Capsule* about 15 mm. long.

Distribution ‡.—South EUROPE. From isolated stations in Albania and Hercegovina *E. alpinum* spreads northward over the highlands of Serbia and Bosnia, having here its area of greatest abundance, is apparently very local and rare in south-west Croatia, reappears in north Croatia and north-east Istria, becomes fairly widespread in Carniola north to Celje, and then spreads westward across north Italy along the southern fringe (prealpi) of the Julian Alps and Friuli into the southern Dolomites, here becoming fairly widespread and ascending, from around Bassano and Verona through the Val Sugana and

‡ In preparing the following account I have used, in addition to herbarium records, information kindly supplied by correspondents, notably A. Béguinot (Genova), A. Forti † (Verona), L. Glišić (Beograd), Ivo Horvat (Zagreb), K. Maly (Sarajevo), O. Mattioli (Turin), and V. Val Nero (Verona); the absence of any other *Epimedium* or similar plant from this region makes it possible to accept such records. Of the many specimens seen at Florence, Prague, Vienna, and elsewhere I have considered it necessary to cite only a few well-distributed exsiccata.

Val Lagarina, into the Tirol along both sides of the valley of the Adige (Etsch) up to Salorno, but halting to the west at Monte Baldo by the Lago di Garda ; it also occurs in two groups of wooded hills, the Colli Euganei near Padua and the Monti Berici near Vicenza, which rise like islands from the valley of the Po ; in Lombardia it has only a few isolated stations by the Lago d'Iseo and the Lago di Como, but in the lower regions of the western Alps at the north-west corner of Piemonte between Lago Maggiore and Ivrea it again becomes fairly abundant and occurs in the hills of central Piemonte at Casale. It is also recorded to the south at Garessio and in the Etruscan Apennines near Monte Cimone, but these need confirmation. Evidently *E. alpinum* is a plant which has spread from the Balkan peninsula—an area of refuge during the Quaternary Ice-Age—into north Italy up the valley of the Po and thence penetrated into the southern valleys of the Alps ; its range is paralleled in whole or in part by various other species with Balkan affinities, e.g. *Lilium carniolicum* Bernhardi, *Festuca spectabilis* Jan, *Genista sericea* Linn., *Omphalodes verna* Moench, *Saxifraga elatior* Mert. & Koch, *Valeriana saxatilis* Linn. (cf. Pampanini, 1903). Its altitudinal range is mostly between 100 and 1000 m., its customary habitat the shade of mixed deciduous woods dominated by *Quercus* and *Castanea*, where it associates with such woodland herbs as *Isopyrum*, *Helleborus*, *Anemone nemorosa* Linn., *Dentaria*, *Corydalis cava* Schweigg., *C. solida* Sw., *Oxalis Acetosella* Linn., *Primula vulgaris* Huds. (*P. acaulis* Hill), *Asarum*, *Euphorbia carniolica* Jacq., *Allium ursinum* Linn., *Erythronium Dens-canis* Linn., etc. ; in Bosnia and Croatia, however, it occurs in woods of beech (*Fagus silvatica* Linn.) and of conifers (*Abies alba* Mill., *Picea Abies* (Linn.) Karst., *Pinus nigra* Arnold), and it ascends to 1250–1300 m. in south-west Serbia (cf. F. A. Novák in Preslia, v. p. 97 ; 1927) and to 1500 m. on the Veliki Stolak in east Bosnia (K. Maly, in litt.). Although sometimes described as a silicicolous species, it also grows on limestone, werfen beds, and serpentine ; since its rhizome and roots lie within the upper six inches of woodland soil, it is probably little affected by the formation beneath. In neither ecology nor general range is it an alpine species. Under cultivation it thrives in almost any soil and is hardy so far north as Sweden and Scotland ; it has also been naturalized here and there in Belgium, Czechoslovakia, France, Germany, and Switzerland. I have seen a specimen, certainly of *E. alpinum* and not of *E. pubigerum* as might more probably have been expected, from 'Regio Transcaspica, Krasaswodsk' (*Sintenis*, Iter Transcasp., 1901, in herb. Copenhagen !) and another from 'Rossia media Orient. ad Biljinbaja, mtes Uralenses, Juni 1874, leg. Clerc' (herb. Manchester Mus. !), both so far outside the known range of *E. alpinum* that its occurrence as an indigenous plant in these places seems highly improbable.

Type-locality.—'In Alpium Euganeorum, Ligurinorum, Pontebarum umbrosis' (Linn. loc. cit.; 1753). The species was known to Linnaeus only from garden material. Its Italian distribution he gleaned from previous literature. The Colli Euganei near Padua, from which region it was introduced

into cultivation, may accordingly be taken as the type-locality. The occurrence of *E. alpinum* in the Friuli (clim Pontabia) was first recorded by John Ray (Obs. p. 147, Cat. Pl. p. 42 ; 1673), who observed it near Pontebba in 1663. Linnaeus and Ray supposed their species to be the same as that recorded by Cesalpino (De plantis, p. 598 ; 1583) from Liguria, a dry region wherein *E. alpinum* has never been collected, but the plant which Cesalpino identified with Dioscorides' Ἐπιμήδων is, as his herbarium in Florence (cf. Caruel, Illus. Hort. sicc. Caesalp., p. 104 ; 1858) reveals, not *E. alpinum* but a very different plant widespread in Liguria, *Anemone Hepatica* Linn. (*Hepatica nobilis* Mill.).

ALBANIA :—Reported in 1906 from a damp gully north of Tirana (Janchen in Oestr. bot. Zeitschr. LXVI, p. 386) ; now known from Mt. Jalitza Ilum (Dgalica Ilum), where an Albanian schoolmaster, Rjok Zojsi, collected it in 1937 (herb. Stearn !), from Frenkth (41° 33' N., 19° 55' E.) near Kruja, at 800 m. (*Markgraf*, 1159 ; B !), from Sureli (41° 20' N., 19° 55' E.) near Tirana, at 400 m. (*Markgraf* 349 ; B !), and from Librash (41° 13' N., 20° 21' E.) at 1200 m. (cf. *Markgraf* in Bibl. Bot., xxvi, 105, p. 36 ; 1932).

JUGOSLAVIA (Yugoslavia)† :—Serbia (i.e. south Dunavska, mid-west Morav-ska and east Drinska banov.) : in the north-west fairly widespread and recorded from near Kijevo south of Beograd (Belgrade), Jagodina (43° 59' N., 21° 15' E.), this being the most eastern station known, Levač, Gruza, Mt. Kotlenik, Mt. Stolovi, Mt. Rudnik, Valjevo, Požega and Mt. Mokra Gora (L. Glišić, in litt.). Bosnia (i.e. west Drinska, Vrbaska and north Zetska banov.) : fairly widespread, occurring on the northern outskirts of the mountainous region near Tuzla, Karanovac, Derventa, Kobas, etc., and penetrating inward along river valleys, e.g. up the valley of the Drina and its tributaries by way of Zvornik, Srebrenica, Višegrad, Mokra Gora (Serbia) to Foča and Sūha, up the valley of the Bosna and its tributaries by way of Doboј, Tešanj, Maglaj, Zepče, Zenica, Lašva to Travnik, Vares and Sarajevo, and up the valley of the Vrbas from Banjaluka to Jajce and westward to Varcas ; cf. G. Beck-Mannagetta, Fl. Bosne, Hercegov. II (7), p. 42 (1916). Exsiccata :—Magnier, Fl. Sel. Exsicc. no. 2638. Hercegovina (i.e. extreme south-east Primorska banovina) : at Velez near Mostar (K. Maly, in litt.) ; its rarity is evidently related to the Mediterranean climate of Hercegovina, a region exposed in winter to the cold and violent bora and in summer very hot and dry ; Bosnia, where on the other hand *E. alpinum* abounds, has a milder, more even climate, with abundant rainfall spread fairly evenly over the whole year (Turrill, 1929, p. 54). Slavonia (east Savska banovina) : uncommon, apparently only in the high country at Požegn and Krndija Gora. Croatia (west Savska banovina) : fairly widespread in the north, from Plitvice through Slunj, Ogulin, Vrbovsko, etc., along the edge of the Velika and Mala Kapela north to Čabor, and from

† The provincial divisions employed here are those shown in J. C. Bartholomew, 'Times Survey Atlas', maps 47 and 36 (1922), their approximate equivalents in the territorially re-organized kingdom (1929) being indicated in brackets.

Petrinja and the neighbourhood of Zagreb (Zapnešic, Tuškanec, Samobor, etc.) westward to Bjelolasica, Delnice, Fućine and Kastav and southward to near Kamić (I. Horvat, in litt.). Carniola (Dravska banovina): fairly widespread in the south, occurring near Tschernembl, Metlika (Möttling), the Gorjanci (Uskoken) range, Novo Mesto (Rudolfswerth), Zužemberk (Seisenberg), Nassenfuss, Brezice (Rann), Krško (Gurkfeld), Lichtenwald, Zidanimost (Steinbrück), Rimske Toplice (Römerbad), Laško (Tüffer), and Celje (Cilli), this being, with Caporetto, Mte. Verzegnis and Arnoldstein, among its most northern stations; cf. Paulin, Sched. Fl. Exsicc. Carniol., no. 67; Hayek, Fl. Steiermark, I, p. 358 (1908). Exsiccata:—Paulin, Fl. Exsicc. Carniol. no. 67; Hayek, Fl. Stir. Exsicc. no. 19; Reichenbach, Fl. Germ. Exsicc., no. 1283.



MAP 5.—Distribution of *Epimedium alpinum* (South Europe)
(dots indicate stations).

AUSTRIA:—Only in south Carinthia (Kärnten) near Arnoldstein; cf. Hegi, Fl. Mittel-Eur. IV, I, p. 10 (1913).

ITALY:—Venezia Giulia in north-east Istria, near Abbazia and between Mounts Plavnik and Sissal not far from Mte. Maggiore, and in the Alpi Giulie (Julian Alps) from the Wippach valley near Gorizia (Görz) northward up the Isonzo valley to Caporetto; cf. A. M. Smith in Verhandl. Zool.-bot. Ges. Wien, XXVIII, p. 335 (1878); Pospichal, Fl. oest. Küstenl. II, I, p. 67 (1898). Exsiccata:—A. M. Smith, 1860, sine no.; C. Marchesetti, 1892, sine no. Venezia and Venezia Tridentina (Trentino), fairly widespread in the wooded submontane region of the Friuli and Carnia north of Udine, with stations in the Natizone valley and at S. Daniele, Mte. Verzegnis, etc., extending westward to Vittorio and Conegliano and up the Piave valley to Feltre and Agordo, with many stations in the valleys between Verona to the south, the

Val Sugana to the north, and Mte. Baldo to the west, the Tirolean valley of the Adige (Etsch) being ascended nearly as far north as Salorno; separated from these by the lowlands of the valley of the Po are colonies in the Monti Berici south of Vicenza and the Colli Euganei east of Padua (Padova), while an extreme but probably unnatural station is near Chioggia by the Venetian lagoon; cf. Gortani, Fl. Friulana, II, p. 217 (1906); Saccardo, Fl. Tarvis., p. 141 (1917), ex Atti R. Ist. Veneto, LXXVI; Goiran, Fl. Veron., II, p. 33 (1897); Béguinot in Bull. Soc. bot. Ital., 1904, p. 392; Béguinot, Fl. Padovana, II, p. 346 (1910); Pampanini, Essai, p. 96 (1903); Dalla-Torre and Sarnheim, Farn. Blüten. Tirol, II, p. 306 (1909); Hegi, Fl. Mittel-Eur., IV, I, p. 10 (1913). Exsiccata:—Fiori, Béguinot and Pampanini, Fl. Ital. Exsiccat. n. 574; Dufour, Soc. franç., 1931, Exsiccat. n. 6291; A. Kerner, sine no.; P. Porta, 1871, sine no.; F. Schultz, Herb. norm. n.s. no. 1014. Lombardia: rare but recorded from Mte. Guglielmo, east of the Lago d'Iseo, by E. Zersi, Prosp. Piante Brescia, p. 18 (1871), who states that the mountain folk use its roots or rhizomes to purge their cows after calving, and recorded from the Intelvi valley, between Pona and Laino, north of Mte. Generoso, by Comolli, Fl. Comense, I, p. 203 (1834). Piemonte: fairly abundant in the north-west foot-hills at Gattinara, Grignasco, Borgosesia, Biella, Viverone, and Borgomasino and also in central Piemonte at Casale Monferrato. Allioni's record of it from near Garessio ('in montibus Garrexi') needs confirmation. Exsiccata:—A. Negri, Soc. Helv. 1873. Liguria: indicated from here in error by Ray, Linné, and Komarov (cf. supra); no trustworthy evidence is available, while climatic conditions make its presence unlikely. Emilia, recorded 'in Apennino Mugellano et prope Marradium' by Savi, Bot. Etruse., II, p. 96 (1815), and from 'Fiumalbo, alle falde del Cimone' by Gibelli and Piotta, Fl. Moden., p. 15 (1882), ex Atti Soc. nat. Modena, ser. 3, I, but neither in the rich Italian herbaria of Florence, Pisa, Rome, nor elsewhere did I find any specimens from the Apennines except Jan, no. 115, 1 (vaguely labelled 'in Apenninis'); Mte. Cimone ($44^{\circ} 11' N.$, $10^{\circ} 44' E.$) is on almost the same longitude as Caprino $45^{\circ} 38' N.$, $10^{\circ} 48' E.$), the most western station of the Venetian area of *E. alpinum*. If the presence of *E. alpinum* on the north side of the Apennines is confirmed, this together with its presence in the Colli Euganei, Monti Berici, and Monferrato will support the supposition that *E. alpinum* spread into north Italy when the lowlands of the Po valley were forested and that its discontinuous range in the Alpine foot-hills is a consequence of its being driven to take refuge in them by the lowlands becoming unsuitable: how such a range could have been attained by migration along the lower region of the southern Alps in the altitudinal zone it has to-day is difficult to see, although the effect of man's deforestation of Italy as a factor in part responsible for the present wide gaps in its range must also be remembered.

Being of easy cultivation *E. alpinum*, the type-species of the genus *Epimedium*, early found its way into gardens from north Italy. Luigi Anguillaria had observed it near Vicenza by 1560, and Francesco Calzolari on Mte. Baldo by

1566 ; Pena and L'Obel received it from the garden of a Venetian apothecary, Giovanni Pomelli, when in Italy between 1558 and 1568 ; by 1576 it was in Belgian gardens ; Camerarius the younger grew it at Nürnberg in 1588 and the French herbalist Jean Robin of Paris by 1597 had sent it to Gerard in London who 'thought good to call it Barren woort in English ; not because that Dioscorides saith it is barren both of flowers and seedes, but because as some authors affirme, being drunke it is an enimie to conception'. The plant varies much as to general size in response to local conditions and slightly as to flower-size. *E. rubrum* C. Morr. (*E. alpinum* var. *rubrum* Hook. f.), which Franchet and Komarov describe as being merely a large-flowered variant of *E. alpinum*, is here considered a garden hybrid between *E. alpinum* and *E. grandiflorum*, while *E. alpinum* var. *pubigerum* DC. (*E. pubigerum* Morr. & Dene) is specifically distinct from *E. alpinum*. Linnaeus apparently received *E. alpinum* from the Empress Catherine the Great of Russia and accordingly planted it in his 'Siberian garden' at Hammarby, about 7 miles from Uppsala, where it now grows in great profusion. Here, as in the old Linnaean Garden and in the University Botanic Garden at Uppsala, it endures the winter without protection ; Mr. Carl G. Alm, to whom I am indebted for plants from Hammarby, states that he has seen *E. alpinum* in a garden as far north as Hernoeshand (62° 37' N., 17° 58' E.), but it was probably protected there by a spruce covering in winter.

4. *E. PUBIGERUM* (De Candolle) Morren & Decaisne.

? *E. Orientale*, *flore albo* Tournefort, Corollarium, p. 17 (1703). ? *E. Orientale*, *flore ex albo flavescente* Tourn., loc. cit. (1703). *E. alpinum* var. *pubigerum* DC. (!) Veg. Syst. II, p. 28 (1821) : Baker in Gard. Chron. N.S. XIII, p. 620 (1880) : Franch. in Bull. Soc. Bot. France, XXXIII, p. 107 (1886). *E. pubigerum* (DC.) Morr. & Dene (!) in Ann. Sci. Nat. Bot. ser 2, II, p. 355 (1834) : Seringe, Fl. Jard. III, 273 (1849) : Boiss. Fl. Or. I, p. 101 (1867) : Rouy, Illust. Pl. Europ. fasc. VI, p. t. 127 (1896) : N. Busch in Fl. Cauc. Crit. III, 3, p. 209 (1903) : Komarov in Acta Hort. Petrop. XXIX, p. 131 (1908) : Stefanoff & Stojanoff, Fl. Bulgarie, I, p. 468, fig. 565 (1925), in Annaire Archiv Minist. Agric. Bulg. IV ; Turrill in Hooker's Ic. XXXII (5th ser. II), t. 3116 (1927) : Turrill, Pl. Life Balkan Penins. pp. 139, 269, 420, 463 (1929) : Grossheim, Fl. Kavkaza, II, p. 124 (1930) : Stefanoff & Jordanoff in Engl. Bot. Jahrb., LXIV, p. 443 (1931) : Bornmüller in Fedde, Repert. Sp. Nov. Beih. LXXXIX, p. 19 (1936). '*E. alpinum* Linn.' Sibthorp & Smith, Fl. Graeca, II, p. 39 tantum quoad plant. Constantinop. (1813) : Ledeb. Fl. Rossica, I, p. 81 quoad plant. Caucas. (1841), non Linn.

Figures.—Rouy, Illust. VI, t. 127 ; Hooker's Ic. t. 3116 ; Stef. & Stojan. Fl. Bulg. I, fig. 565.

Plant in flower 20–75 cm. high. Rhizome comparatively short and stout, nodose, c. 5 mm. or more thick. Leaves basal and cauline, usually binate,

occasionally trifoliolate or trinernate; *leaflets* ovate to broadly ovate or almost rotund, the tip acute, the margin sparsely spinous, the base deeply cordate, firm in texture, dark green above, blue-glaucous and persistently pubescent beneath with crowded soft white hairs usually very dense at the insertion of the petiole, about 4·5 cm. long, 2·5 cm. broad, but attaining 9·5 cm. long, 6 cm. broad. *Flowering stem* bearing one biernate leaf; *inflorescence* compound, loose, very glandular, usually many- (12-30) flowered, overtopping the stem-leaf; lower peduncles often 3-5-flowered; *pedicels* usually 3-10 (sometimes up to 20) mm. long. *Flowers* 8-12 mm. across, pale. *Outer sepals* red-tinted, broadly ovate, blunt, about 3 mm. long, sometimes with short glandular red-tipped hairs. *Inner sepals* narrowly ovate, blunt, very concave, pale rose or nearly white, 5-7 mm. long, 2 mm. broad. *Petals* slightly shorter than the inner sepals, slipper-like, cylindric, blunt, 3·5-4 mm. long, canary yellow, with no laminae. *Stamens* protruding, about 3 mm. long; *anthers* about 2 mm. long. *Capsule* short and fairly plump, 5-15 mm. long, including the persistent style.

Distribution.—Western TRANSCAUCASIA, north ASIA MINOR, and south-east EUROPE, extending from the Batumskaya oblast of Georgia (Adjar valley) along the wooded Black Sea slopes of north Turkey (prov. Trebizond and Kastambuli; cf. Krause in Engl. Bot. Jahrb. LXV, p. 348; 1932) to east Thrace and the Strandja mountains (cf. Turrill, Balkan Peninsula, pp. 14, 139; 1929) of south-east Bulgaria, where it occurs sporadically in damp deciduous woods of *Fagus orientalis* Lipsky and the other Pontic trees and shrubs (e.g. *Rhododendron ponticum* Linn., *Daphne pontica* Linn., *Prunus Laurocerasus* Linn., *Mespilus germanica* Linn., *Vaccinium Arctostaphylos* Linn., etc.) which cover the sides of the deep and narrow valleys; the herbaceous flora here is open, often scanty, and consists of few species, e.g. *Cyclamen ibericum* Goldie, *Trachystemon orientale* (Willd.) D. Don, *Orobis aureus* Steven, etc., among which *E. pubigerum* frequently predominates and thrives luxuriantly (fide B. Stefanoff in litt.). Its Asiatic area corresponds more or less to the coast regions of the ancient kingdoms of Colchis, Pontus, Paphlagonia, and Bithynia. The climate is colder in winter and cooler and moister in summer than that of typical Mediterranean districts; rain falls throughout the year, becoming especially high eastward to Rhize.

To *E. pubigerum* belong Formánek's specimens (!) from 'Boujuk-Dure in Turcia europaea' and 'Beikos et Adampol in Asia Minor (Bithynia)' enumerated as *E. alpinum* by Vandas (Reliq. Formánek. p. 15; 1909). Rouy records *E. pubigerum* from Bosnia ('Travnik, Brandis') but Brandis' specimens (*Magnier*, Fl. Select. Exsicc. 2638 !) belong to *E. alpinum*, while records of *E. alpinum* from Thrace refer to *E. pubigerum*.

Type-locality.—'Circa Constantinopolim collegit cl. Olivier' (De Candolle, loc. cit.).

BULGARIA :—Mt. Strandja in wet forests of *Fagus orientalis*, v. 1921, *Stojanoff & Stefanoff* 874 (K. !); cult. in Sofia botanic garden, originally obtained from Strandja, *Stefanoff* (hb. Stearn !). Merzevo near mt. Trnovo, *Krist* (Brno ! hb. Stearn !), near Urgari at mt. Trnovo, *Krist* (Brno ! hb. Stearn !). TURKEY IN EUROPE (Thrace) :—Constantinople, *Olivier & Bruguière* (Gen ! type ; P. !), *Heldreich* 1102 (B. !), *Aucher-Eloy* 392 (K. ! P. ! F. ! B.M. ! Gen. ! Boiss. !); margin of wood near Zekerikeuy, *Aznavour* (Manchester !); in groves about Byzantium [Istanbul] at Therapia, *Dumont d'Urville* (P. ! Gen. !); at Byzantium in the Belgrade forest, *Bornmüller*, Iter Anatol. 4035 (B. ! K. ! Weimar ! Gen. ! Boiss. !); on bushy hills between the Baghtschehoui and Belgrad districts near Pyrgos, *Degen*, Iter Turec. (K. ! F. ! Gen. ! Boiss. ! Weimar !); Buyukdere, *W. Barbey* (Boiss ! Gen. !) *Formanek* (Brno !), Belgrade Forest, at 400 ft., among heath and scrub, *E. K. Balls*, 601 (hb. Stearn !).

TURKEY IN ASIA (Bithynia, Paphlagonia, Pontus) :—Beikos and Adampol, *Formanék* (two small not very characteristic leaves ; Brno !); Ada Bazar (Adapazari), 50–100 m., *Warburg & Endlich*, Iter Pryg. II, p. 4 (B. ! hb. Stearn !); Alemdagh, 1846, *Noé* (K. !); near Anadoli Kawak, III, 1925, *Korner* 1 (fide *Krause*, loc. cit.) ; Wilajet Kastambuli, Kure-Nahas, in wood at Erzrerhervit, *Sintenis*, Iter Orient. 3768 (P. ! Weimar ! D. U. Prag ! B.M. ! Zürich ! Boiss. !); mt. Karadagh between Sausum and Amasia, 500–700 m., *Bornmüller*, Pl. Anatol. Orient. 1863 (K. ! Weimar ! B. ! Boiss. !); wooded valley to the west of Kerasun at 50 m., *Krause* 1801 (fide *Krause*, loc. cit.) ; Fol Koei, c. 1100 m., *H. Handel-Mazzetti*, 409 (V. !); near Trebizond, *Bourgeau*, Pl. Armen. 9 (K. ! B. ! F. ! P. ! Cantab. ! Gen. ! Manchester !), Trebizond, in the brushwood above the town, *Bourgeau* 24 (Boiss. !); common near Trebizond, in scrub-woodland of *Rhododendron*, *Carpinus*, *Vaccinium*, etc., usually below 2,000 ft., extremely luxuriant and abundant where the woodland has been burnt away ; climate here very damp with frequent fog, *Balfour-Goultay* (Cantab. !); underwood near the shore of the Black Sea at Rhize, Lazistan, *Balansa* (Boiss. !).

GEORGIA, U.S.S.R. (Colchis) :—Abkhasia : Batum, *Radde* 9 (Boiss. !); in woods by the river Czakawa near Batum, *Czerniawsky* (K. !). Adzhar : Adjaria in Anticaucasia, between Batum and Akhabzikh in shady thickets, *Sommier & Levier*, Iter Caucasia. 8 (B. ! F. !); between Khula (Chula) et Danais-Paraoul in middle wooded region, *Sommier & Levier*, 48 (Boiss. ! F. !); Adzharia, mt. Kalwa, 1893, *Alboff*, Pl. Adj. 215 (B. ! K. ! N.Y. !), 210 (P. !), 212 (P. !), 214 (Boiss. !), 218 (Boiss. ! Weimar !).

Despite Franchet's assertion that *E. pubigerum* differs from *E. alpinum* only in the denser and more persistent pubescence of its leaflets, the two are really very distinct. The rhizome of *E. pubigerum* forms a compact woody mass which grows slowly, as the new shoots are short and thus arise near one another, while *E. alpinum* has more elongated slender rhizomes, sometimes growing three or more inches in a season, and under favourable conditions runs into wide patches. The leaflets of *E. pubigerum* are firmer in texture,

as well as more pubescent beneath, than those of *E. alpinum* †. The relation of stem-leaf and inflorescence provides another obvious contrast. In *E. alpinum* the inflorescence is shorter than the stem-leaf and bends away from the common stem, so that (in the living plant) the dark red-sepalled flowers are more or less hidden by the foliage. In *E. pubigerum* the erect pale-flowered inflorescence rises above the stem-leaf. The two species also differ in distribution, *E. alpinum* being a south-central European plant (Italy, Jugoslavia), while *E. pubigerum* belongs essentially to north Asia Minor, although occurring within a limited area (Thrace, Bulgaria) on the east side of the Balkan peninsula.

Sibthorp and Smith's plate (Fl. Graeca, II, t. 150, as *E. alpinum*), which Franchet and Komarov cite as representing *E. pubigerum*, is actually an excellent picture of true *E. alpinum* probably made from a cultivated plant on Sibthorp's return to England, though the locality given—'in agro Constantinopolitano'—is the locus classicus of *E. pubigerum*. This species was first introduced into English gardens in 1887 by the late Miss Ellen Ann Willmott, who obtained it from Boissier's garden at Geneva, his stock probably coming from Istanbul (Constantinople); recently it has been introduced from the Strandja by Professors Stojanoff and Stefanoff and from Istanbul and Trabzon (Trebizond) by Mr. E. K. Balls. It is a graceful and uncommon plant, of compact growth, suited to a shady rock garden.

Series *Macrocerae*.

Epimedium sect. *Macroceras* Morr. & Dene in Ann. Sci. Nat. Bot. ser 2, II, p. 349 (1834); Spach, Hist. Veg. Phan. VIII, p. 59 (1839); Fisch. & Mey. Sert. Petrop. sub t. 1 (1846); Baill. Adansonia, II, p. 270 (1862); Hist. Pl. III, p. 56 in adnot. (1871). *Endoplectris* † Rafin. Fl. Tellur. III, p. 56 (1837). *Epimedium* subgen. *Macroceras* Seringe, Fl. Jardins. III, p. 275 (1849).

Flowers 2-4.5 cm. across. *Inner sepals* narrowly ovate to lanceolate, flat. *Petals* longer than the inner sepals, with elongated slender spurs and distinct petaloid laminae, enclosing the *stamens*.

This group occurs in Japan, Korea, Manchuria, and Far Eastern Russia.

Type-species:—*E. grandiflorum* C. Morr.

5. *E. GRANDIFLORUM* C. Morren, sensu lato. (Pl. 31, fig. 1.)

E. grandiflorum C. Morr. in L'Horticult. Belge, II, p. 141, t. 35 A (Sept. 1834). *E. violaceum* C. Morr., op. cit. p. 142, t. 35 B (1834). *E. macranthum* Morr. &

† In cultivation the leaves of *E. alpinum* wither by November, but those of *E. pubigerum* remain green the winter through, both in the garden and in nature. On April 4, 1934, I received living material from the type-locality (Istanbul) collected by Mr. E. K. Balls (no. 601) on March 31, 1934, with the previous year's leaves still perfectly firm and green.

‡ From ἐνδός, 'within', 'in the house', etc., πλήκτρον, 'a cock's spur', the inner part of the flower bearing spurs, as indicated by Rafinesque himself:—'ENDOPLECTRIS R. (inside spurs) another *Epimedium* . . . quite peculiar by the long spurs of petals'.

Dene in Ann. Sci. Nat. Bot. ser. 2, II, p. 352, t. 13 (Dec. 1834) et auct. plur. : Savatier (transl.), Livres Kwa-wi, Herb. IV, no. 5 (1875) : Baker in Gard. Chron. N.S. XIII, p. 683 (1880) : Franch. in Bull. Soc. Bot. France, XXXIII, p. 105 (1886) : T. Ito in Journ. Linn. Soc., Bot. XXII, p. 430 p.p. (1887) : Voss, Vilmorin's Blumeng., I, p. 51 p.p. (1896) : W. Miller in L. H. Bailey, Cycl. Am. Hort. II, p. 536 p.p. (1900) ; and Stand. Cycl. Hort. II, p. 1122 p.p. (1914) : Komarov, Fl. Manschur. II, in Acta Hort. Petrop. XXII, p. 324 (1903) : Makino in Inuma, Somoku Dzus. ed. 3, II, p. 125, t. 45 (1907) : Komarov in Acta Hort. Petrop. XXIX, p. 131 (1908) : Matsumura, Index Pl. Jap. II, (Dicot.), p. 130 (1912) : Kudo in Jap. Journ. Bot. II, p. 259 (1925) : Wehrhahn, Gartenstauden, I, p. 454 p.p. in textu, 'E. sinense' in icona (1930) : Ichimura, Important med. pl. Japan, t. 34 (1932). ? E. Musschianum Morr. & Dcne, op. cit. p. 353 (1834). *Endoplectris tricolor* Rafin. Fl. Tellur. III, p. 57, no. 637 (1837). *E. longifolium* Dene in Revue Hort. ser. 4, III, p. 285 (1854). *E. macranthum* var. *Thunbergianum* Miq. in Ann. Mus. Lugd. Batav. II, p. 70 ? p.p. (1865). *E. koreanum* Nakai, Fl. sylvat. Koreana, XXI, pp. 55, 60, 63 (1936) : B. Fedtsch. in Komarov, Fl. U.R.S.S. VII, p. 544 excl. pl. Ussur. (1937).

Plant in flower 12–35 cm. high. Rhizome elongated, 3–5 mm. thick. Leaves basal and caudine, biernate or triternate ; leaflets narrowly ovate to broadly ovate, the tip acute or acuminate, the margin very spinous-serrate, the base deeply cordate with usually rounded lobes, membranous in texture, glaucous beneath, bronzy or light green when young, at length glabrous or sparsely pubescent beneath, 3–13 cm. long, 2–8 cm. broad. Flowering stem bearing one biernate or triternate leaf ; inflorescence simple or compound with the lower peduncles 3-flowered, loose, glabrous or rarely pilose, 4–16-flowered, usually overtopping the stem-leaf ; pedicels 1–2 cm. long. Flowers 2–4.5 cm. across, white, pale yellow, deep rose, or violet. Outer sepals red-tinged, oblong, 4–5 mm. long. Inner sepals narrowly ovate to lanceolate, acute, flat, 8–18 mm. long, 3–6 mm. broad. Petals usually much longer than the inner sepals, with distinct petaloid rounded laminae 5–8 mm. deep and slender tapering subulate spurs 1–2 cm. long. Stamens included, 5 mm. long ; anthers 4 mm. long.

Distribution.—JAPAN (Honshu and Hokkaido), south MANCHURIA, and north KOREA, locally abundant in woods.

Type-locality :—‘Japon’, whence imported into European gardens by von Siebold.

JAPAN :—Hokkaido (Yezo) ; prov. Oshima at Fukuyama (*Faurie* !) and Hakodate (*Albrecht* !) ; prov. Shiribeshi, Ishikari and Teshio (fide Kudo, loc. cit.). Honshu (the main island of Japan) ; prov. Aomori (Mutsu) near Aomori (*Faurie* !), Kominato (*Faurie* !) ; prov. Akita (Ugo) near Akita (*Faurie* !) ; prov. Miyagi (Rikuzen) near Sendai (*Yasuda* !) ; prov. Fukushima (Iwaki) near Shirakawa (*Faurie* !) ; prov. Tochigi (Himotsuke) near Nikko (*Rein* !),

Utsunomiya (*Faurie* !); prov. Shimosa near Matsudo (*Narita* !); prov. Musashi near Tokyo (*Faurie* ! *Hildendorf* !), Meguro (*Saida* !), Kokubuija (*Takeda* !), Chichibu (K. ! P. !), Ookanyama (*Watanabe* !), Mitake (fide *Matsumura*, loc. cit.); prov. Kanagawa (Sagami) near Mio-mura (*Bisset* !), in hills of Hakone (*Savatier* ! *Faurie* !); prov. Shiga (Omi) by Lake Biwa (*Challenger Exped.* !) at Sidsugatake (fide *Matsumura*, loc. cit.); prov. Yamashiro at Kuramayama (*Rein* !). Ryukyu (Liukiu, fide *Matsumura*, loc. cit.).

MANCHURIA (Manchoukuo):—Prov. Fengtien: Laoyeh and other hills near Moukden (*James* in K. !), Tangho-ko, Sungari River (*James* in K. !), 'Soonghwa-hien, Black Bear Valley' (*Ross* in K. !), Chikuanshan (*Martin* in München!), 'Changdien to Quangdien' (*Ross* in K. !); Feng-huan, Wu-lung-pei and Kwantien (fide Yabe, Enum. pl. S. Manch. p. 54; 1912).

KOREA (Chosen):—Since this account was prepared, Nakai has separated the Korean-Manchurian plant—referred to *E. macranthum* by previous authors, e.g. Forbes and Hemsley (1886), Komarov (1904), Nakai (1911), and Mori (1922)—as a distinct species, *E. koreanum* Nakai, distinguished by its supposedly larger size and yellowish flowers:—‘*Epimedio macrantho* affine sed ex omnibus partibus majus et flores flavidii’ (Nakai, loc. cit.; 1936). He describes the rhizome of this Korean plant as 3–5 mm. thick, the terminal leaflet of its biennial basal leaves as 5–10 cm. long, 3·3–7·2 cm. broad, the lateral leaflets 5–13·5 cm. long, 3·5–7·5 cm. broad, those of the stem leaves a little smaller, the pedicels 8–15 mm. long, the inner sepals yellowish and 8–10 mm. long, the petals yellowish, long-spurred, with the lamina 7–10 mm. high, the spur 18–20 mm. long, and the stamens 4–5 mm. long. There is little in these measurements and nothing in the limited herbarium material seen from Korea and Manchuria to suggest that the Korean-Manchurian plant is constantly larger than the north Japanese plant or that they differ in other ways; Faurie’s robust specimens from Aomori in Honshu, and Maximowicz’s from Hakodate in Hokkaido, for example, have leaflets and flowers quite as big as those of the Korean plant. Nor does any constant difference in flower-colour appear to separate the island and mainland populations, since yellow-flowered forms are recorded from Japan. *E. koreanum* is accordingly here regarded as conspecific with *E. grandiflorum*. It is evidently widespread in northern Korea. According to Komarov, it covers wide spaces on wooded slopes along the upper course of the Yalu river. Nakai records it from prov. Heian-hoku (Heihoku or north Phyeng-an) at mount Hakuhekizan (type-locality of *E. koreanum*) and Sakusyu; prov. Heian-nan (Heinan or south Phyeng-an) at Neien and mount Taiseizan (?=Taikakuzan); prov. Kankyo-nan (Kannan or south Ham-gyang) near Genzan, mount Matenrei, Kozan (Komarov 736!) and between Futempo and Hotaido; prov. Kankyo-hoku (Kanhoku or north Ham-gyeng) at Seisin and Shuotu-onmen; prov. Kogen, in the north, between Kenfuturo and Shasori. Mill’s material (n. 14; K !) from ‘Kangkai, Korea’ was presumably collected in prov. Kokai (Hwang-hai).

For horticultural purposes it seems advisable to distinguish the following colour-forms :—

Forma α NORMALE (Voss) Stearn, trans. nov.

E. grandiflorum C. Morr. loc. cit. t. 35 A (Sept. 1834); Seringe, Fl. Jardins, III, p. 275 (1849), sensu stricto. *E. macranthum* Morr. & Dene, loc. cit. (Dec. 1834): Lindley in Bot. Reg. XXII, t. 1906* (1836): Maund & Henslow, Botanist, II, t. 90* (1838); Paxton, Mag. Bot. V, 151 cum icono * (1838): Spach, Hist. Veg. Phan. VIII, p. 58 (1839): Loudon, Ladies' Fl. Gard. Orn. Per. I, t. 13* (1843): Lescuyer in Hort. Franc. 1854, p. 146, t. 13, fig. 1* (1854); Pucci in Bull. Soc. Tosc. Ort. Firenze, XVII, p. 364, t. 12* (1892): Klein, Gartenblumen, I, p. 31 p.p. (1926), sensu stricto. ? *E. Musschianum* Morr. & Dene, loc. cit. (1834). *Endoplectris tricolor* Rafin. loc. cit. (1837). *E. macranthum* var. *typicum* p.p. et ? *humile* T. Ito, loc. cit. (1887). *E. macranthum* f. *normale* Voss, loc. cit. (1896). *E. macranthum* *album* W. T. Macoun, List Per. Exper. Farm, Ottawa (Cent. Exper. Farm, Ottawa, Bull. ser. 2, no. 5), p. 40 (1908). ? *E. macranthum* var. *Musschianum* (Morr. & Dene) Makino in Bot. Mag. Tokyo, XXIII, p. 143 (1909): Wehrhahn, loc. cit. p.p. quoad syn. (1930): Makino & Nemoto, Fl. Japan, ed. 2, p. 348 (1931). *E. macranthum* var. *normale* Wehrhahn in Bonstedt, Pareys Blumeng. I, p. 621 (1931).

Figures.—Hort. Belg. II, t. 35 A*; Ann. Sci. Nat. Bot. ser. 2, II, t. 13: Bot. Reg. XXII, t. 1906*: Maund, Botanist, II, t. 90*: Paxton, Mag. V, p. 151*: Loudon, Ladies' Fl. Gard. Orn. Per. I, t. 13*: Hort. Franc. 1854, t. 13, fig. 1*: Nicholson, Dict. Hort. I, fig. 714, as '*E. alpinum*': Bull. Soc. Tosc. Ort. XVII, t. 12*: Wehrhahn, Gartenst. I, p. 454, as '*E. sinense*': Iinuma, Somoku Dzus. II, p. 46: Klein, Gartenbl. I, p. 31*: Gardening Illust. LIV, p. 31 (1932): Ichimura, Important med. Pl. Japan, t. 34*: Terasaki, Nippon Shokub. Zufu, 152 (1933): Bijutso-shashin-taisei, II, t. 43, leaves only (1936).

This is the original or 'typical' form, having the *inner sepals* ('pétales . . . d'un blanc jaunâtre lavé de rose et violet', C. Morren) tinged with pale violet, especially along the edge, and the *petals* ('nectaires . . . blancs', C. Morren) white.

Forma β FLAVESCENS Stearn, nom. nov.

? *E. longifolium* Dene, loc. cit. (1854). *E. sulphureum* Nakai in litt., non Morren.

Figures.—? Iwasaki, Honzo Dzufu, VI, fol. 11 recto fig. super. sinist., floribus sulphureis (1829): Nishijima, Hi-Shui Hyakku Fu† (1931–34).

This pale-yellow-flowered form is mentioned by the Japanese botanist Shimada alias Yonan (Kwai, Herb. IV, fol. 5) as far back as 1765, when he describes the 'Ikariso' or 'Wooto-kouso' as having 'clear violet, or white, or clear yellow' flowers, accompanying his account with a good but uncoloured figure.

† Coloured plate as *E. macranthum* published in fasc. 2 (t. 10 of copy in Lindley Library).

Decaisne's *E. longifolium* was described from a Japanese painting in Baron Delessert's library and said to be distinguishable from others of the *E. macranthum* group by its long leaves and the colour of its flowers, these being yellowish white ; it has not been possible to trace this painting in Delessert's library now at Geneva.

Forma γ VIOLACEUM (C. Morr.) Stearn.

E. violaceum C. Morr. loc. cit. t. 35 b* (1834) : Morr. & Dene, op. cit. p. 354, t. 12 (1834) : Paxton, Mag. Bot. v, p. 123 cum icone * (1838) : Graham in Edinburgh New Phil. Journ. xxvii, p. 191 (1839), and in Bot. Mag. LXVI, t. 3751* (1839) : Spach, op. cit. p. 60 (1839) : Lindley in Bot. Reg. xxvi, t. 43* (1840) : Seringe, loc. cit. (1849) : Lescuyer, op. cit. t. 13, fig. 2* (1854). *E. violaceum* var. *grandiflorum* Siebold & De Vriese, Fl. Jard. Roy. Pays-Bas, II, p. 81, t. 8* (1859). *E. pumilum* hort. ex Baker, op. cit. p. 68 (1880). *E. macranthum* var. *violaceum* (Morr. & Dene) Franchet, op. cit. p. 106 (1886) : T. Ito, loc. cit. (1887) : W. Miller in Bailey, loc. cit. (1900, 1914) : Makino, loc. cit. (1909) : Wehrhahn, loc. cit. (1930). *E. macranthum* f. *violaceum* Voss, op. cit. t. 5, fig. 20, 1* (1896). *E. grandiflorum* var. *violaceum* (C. Morr.) Stearn in Kew Hand-list Rock Gard. Pl. ed. 4, p. 53 (1934).

Figures.—Hort. Belg. II, t. 35 b* ; Ann. Sci. Nat. Bot. ser. 2, II, t. 12 : Bot. Mag. t. 3751* ; Paxton, Mag. v, p. 123* ; Bot. Reg. xxvi, t. 43* ; Siebold, Fl. Jard. Pays-Bas, II, t. 8* ; Voss, Vilmorin's Blumeng. t. 5, fig. 20, 1* : Hort. Franç. 1854, t. 13, fig. 2* ; Honzo Dzufu, VI, fol. 11 verso*.

A form with light violet petals sometimes not much exceeding the light violet inner sepals.

Forma δ 'ROSE QUEEN'. (Pl. 31, fig. 1.)

E. rubrum Nakai in litt. non Morren.

Figure.—? Iwasaki, Honzo Dzufu, VI, fol. 10 verso, fig. super. *.

A very beautiful form with intense rose flowers known in English gardens as *E. 'Rose Queen'* and *E. macranthum* 'Rose Queen' (cf. Stearn in Gardening Illustr. LIV, p. 31; 1932). The colour seems nearest to the 'carmine cramoisi' or 'crimson-carmine' of Dauthenay's Répertoire des Couleurs, p. 159, no. 1, the petals being slightly paler than the inner sepals, with the spurs becoming white at their tips.

This elegant species is equalled in size of flower only by *E. acuminatum* and its allies. It has long been cultivated in Japan, where it is known as 'Ikariso' or 'Ikari-gusa' (*Ikari*, anchor; *So*, or *Guso*, a plant, the long curved spurs of the flower suggesting the four-fluked grapnel (*Notsuzume Ikari*, four claw anchor) used as an anchor by Japanese fishing boats ; and on its introduction to Europe by von Siebold about 1830 apparently it hybridized with *E. pinnatum*, *E. alpinum*, and *E. diphylloideum*, although hybrids with *E. diphylloideum* seem to have arisen earlier in Japan and were imported to Europe at the same time as the parents ; the resultant plants are described here under $\times E. Youngianum$, $\times E. versicolor$, and $\times E. rubrum$ (pp. 515-525). It is very

variable and plastic as regards general size, form of leaflet, relation in length of inner sepal and petal, flower-colour, etc., and several species have been distinguished on what seem to be minor or fluctuating characters. The genetical basis and distribution of the colour-forms remain to be investigated by Japanese botanists as the plants lose their flower-colour when dried for the herbarium and rarely form seed in European gardens.

According to T. Ishidoya (Chinesische Drogen, I, p. 35, fig. 44; 1933), the dried leaves of this species constitute the tonic drug called 'Ying-yang-huo' (or 'Yenyangho') in Manchuria; in China proper, where *E. grandiflorum* does not occur, the same name is used for leaves of *E. sagittatum*. Other local names of *E. grandiflorum*, kindly transcribed from M. Nakao and K. Kimura, Photogr. Cat. Chinese Drugs, II (Bull. Shanghai Sci. Instit. I, no. 5), pp. 106-9 (1930), by Mr. C. C. Chang, are 'Chi-chu-tso', 'Chi-liang-ching' (thousand-thalers-gold), 'Fang-chang-tsao' (give-up-stick herb; apparently the drug so strengthened an old man that he could discard his stick!), 'Hwang-li-chu', 'Kan-chi-chien', 'Kan-tze', 'Shan-tzi-kiu-yeh-tsao' (three-branches-nine-leaflets-herb), 'Shi-ling-bee' (first-strengthening-the-spleen) and 'Yen-chang-tsao'. According to Mori, Enum. pl. Corea, p. 164 (1922) 'Samchikuyoppul' and 'Umyangkak' are its Korean vernacular names.

5 bis. *E. SEMPERVIRENS* Nakai.

E. sempervirens Nakai ex Maekawa, Alabastra diversa, I, no. 26 in Bot. Mag. Tokyo, XLVI, pp. 582-4, fig. 11 (1932); Nemoto, Fl. Jap. Suppl. 236 (1936). *E. macranthum* var. *hypoglaucum* Makino in Journ. Jap. Bot. VII, 13 (1931)†, fide G. Koidzumi in Acta Phytotaxon. Kyoto, V, p. 126 (1936).

Figure.—Bot. Mag. Tokyo, XLVI, fig. 11 (hab.).

Judging from the original description and figure, *E. sempervirens* is a plant with pure white flowers which agrees with *E. grandiflorum* in almost everything except its evergreen leaves very glaucous beneath. Under cultivation in England the leaves of *E. grandiflorum* perish by November, although certain other species (e.g. *E. pubigerum*) growing in the same conditions persist green until next April. The following description is abbreviated from the prolix original:—

'*Epimedium sempervirens* Nakai sp. nov. in sched. Herb. Imp. Univ. Tokyo. *Planta* perennis 30-40 cm. alta. *Rhizoma* crassum c. 5 mm. latum albescens. . . . *Folia* biennia biternata *foliolo* ovato vel ovato-oblongo basi breviter clauso-cordato apice acuto vel acutissimo margine integerrimo saepe laxe setiferō 2.7-7.5 cm. longo chartaceo supra glaberrimo viridi nitidulo infra venis elevatis glabro opaco glauco-farinoso. *Inflorescentia* terminalis subpaniculata 5.5-7 cm. longa pedunculo glabro aequilonga [in iconē circa 9-flora et subsimplex] *pedicelli* 10-15 mm. longi virides glabri *flos* in finem

† '*Epimedium macranthum* Morr. et Decne var. *hypoglaucum* Makino, nov. var. Leaves green above, white-glaucous beneath. Nom. Nipp. *Urajiro-ikariso* (nov.). Hab. Prov. WAKASA: Mt. Aoba (J. TAKADA!).' (Makino, loc. cit.)

mensis Aprilis patens candissimus lucidiusculus 7–8 mm. longus 25 mm. latus. *Bracteolae* 5 caducae apice obtusae navicularae extus purpureo-punctatae, extrema minor 2 mm. longa linearis-oblonga, intima major 5 mm. longa oblonga late hyalino-marginata; *sepala* [*interiora*] horizontalia patentia membranacea lanceolata apice acutiuscula ca. 11 mm. longa; *petala* longe calcarata; pars lamina obovato-rotundata 7 mm. longa 6 mm. lata apice obtusissima vel truncata margine paulo inflexa, calcar c. 15 mm. longum ex basi laminae rectangulare productum ad apicem sensim attenuatum, parte inferiori $\frac{1}{3}$ valde incurvatum, cetera erecto-ascendens, apice globosum intus sub lente papillosum. *Stamina* 4·4–4·5 mm. longa. . . . Nom. Jap. Tokiwa Ikarisô (nom. nov.).

Hab. [JAPAN] Hondo: prov. Noto, Fugeshi-gun, Yanami oppidi Minami (*H. Hara*, Apr. 19, 1928). [Speciminia ex loco supra citato allata et nunc in Tokyo culta, floret in Apr. 1932—typus].—Suzu-gun, oppido Misaki (*H. Hara*).—prov. Kaga, Kurokabé prope Kanazawa (*M. Takakashi*, Apr. 21, 1932). This is a most remarkable species with biennial coriaceous leaves and snowy flowers' (Nakai ex Maekawa, loc. cit.).

The Korean plant recently described by G. Koidzumi in *Acta Phytotaxonom.*, Kyoto, v, p. 126 (1936), as *E. sempervirens* var. *leucanthum* (a curious name for a plant with yellow flowers) is likewise known to me only from the author's diagnosis \ddagger and seems to be a form (? f. *flavescens*) of *E. grandiflorum* identical with *E. koreanum* Nakai. If Koidzumi's identification of *E. macranthum* var. *hypoglaucum* Makino with *E. sempervirens* is correct, then *E. sempervirens* extends from province Noto to province Wakasa (western Fukui); Aobayama, the type-locality of var. *hypoglaucum*, is about 35° 30' N., 135° 33' E., standing between Takahama and Maizuru.

6. *E. MACROSEPALUM* Stearn, sp. nova. (Pl. 26.)

'*E. macranthum* Morr. et Dene', sec. Komarov & Klobukova-Alisova, Key Pl. Far East U.S.S.R. I, p. 564 (1931), non Morr. et Dene. '*E. koreanum* Nakai', sec. B. Fedtschenko in Komarov, Fl. U.R.S.S. VII, p. 544 (1937) p.p. quoad pl. Ussuriensem, non Nakai; descriptio Fedtschenkoi *E. grandiflorum* Morr. depingit.

Species *grandiflora*; ab *E. grandiflora* Morr. (a quo *E. koreanum* Nakai vix distinctum videtur; cf. p. 481) foliis plerumque 3-foliolatis haud bi- vel tri-ternatis, sepalis interioribus magnis, ab *E. leptorrhizo* Stearn foliolis obtusis, haud longe acuminatis, inter alia distinguitur.

Planta florens c. 25 cm. alta. *Rhizoma* elongatum, tenuissimum, 1–2 mm. crassum. *Folia* plerumque 3-foliolata (sed unum folium basale 7-foliolatum vidi!), *petiolis petiolulisque* sparse pilosis vel subglabris, *petiolis* foliorum basarium 8–14 cm. longis, foliorum caulinorum 5–8 cm. longis, *petiolulis* 2–5·5 cm. longis, *nodis* rubro-pilosis; *foliola* late ovata vel suborbicularia, apice obtusa, margine

\ddagger 'Var. *leucanthum* Koidz. A typo recedit foliolis infra viridibus non glaucis, floribus flavis non albis, caule basi squamis amplis pulchre purpureis. Nom. Jap. *Kibana-ikariso*. *Hab.* Korea: Keikido districtu; Kohkwato (leg. T. Ishidoya! 15 Maj. 1935).'.

leviter undulata et sparse spinosa vel etiam fere integra, basi profunde cordata sinu angusto lobis rotundatis vel acutis \pm contingentibus vel etiam imbricatis, membranacea, supra atroviridia et glabra, subter glauca et pilis brevibus rubris pubescentia, 4-7 cm. longa, 3.3-5.5 cm. lata. *Caulis florifer* monophyllus, folio caulinum 3-foliolato; *inflorescentia* simplex, glabra, pauciflora (floribus 1-3), folio caulinum brevior, c. 5-6 cm. longa; *pedicelli* 2-3 cm. longi vel pedunculus uniflorus 6 cm. longus. *Flores* flavidi, 4 cm. diam. *Sepala exteriora* ignota. *Sepala interiora* oblongo-ovata, obtusa, plana, 20 mm. longa, 8-11 mm. lata. *Petala* longe calcarata, calcari sepulum interius subaequante; lamina petaloidea, rotundata, c. 6 mm. alta; calcar gracile, c. 20 mm. longum. *Stamina* inclusa, 5 mm. longa; antherae 4 mm. longae. *Fructus* (stylo 7 mm. longo inclusu) 35 mm. longus, 3 mm. latus.

Plant in flower c. 25 cm. high. *Rhizome* elongated, 1-2 mm. thick. *Leaves* basal and caudine, normally 3- (less often 7-) foliolate; *leaflets* broadly ovate to almost orbicular, the tip blunt, the margin sparsely spinous-serrate or almost entire, the base deeply cordate with rounded or acute lobes, membranous but firm in texture, above dark green, beneath glaucous and pubescent with short reddish hairs, 4-7 cm. long, 3.3-5.5 cm. broad. *Flowering stem* bearing one 3-foliolate leaf; *inflorescence* simple, glabrous, few-(1-3)-flowered, overtopped by the stem-leaf; *pedicels* 2-3 cm. long, or the peduncle if one-flowered 6 cm. long. *Flowers* large, yellowish, 4 cm. across. *Inner sepals* oblong-ovate, blunt, 20 mm. long, 8-11 mm. broad. *Petals* long-spurred, with distinct petaloid rounded laminae c. 6 mm. high and slender tapering spurs c. 20 mm. long. *Stamens* included, 5 mm. long; anthers 4 mm. long. *Capsule* (including the 7 mm. long style) 35 mm. long, 3 mm. thick.

Distribution.—U.S.S.R., Far Eastern Area, Maritime Province, Southern district, approx. 133°-135° E., 43-44° N., east of Sikhota-Alin main range, in deciduous woodland.

Type-locality.—Tigrovaya station, Suchansk railway.

MARITIME PROVINCE: Preobrazhenski (Preobrajeniya) bay, in deciduous woods, 1907, *Desoulavy* 1049 (Akad. Lenin. !); Tigrovaya station, Suchansk railway, among dense shrubs, rare, 10. vi. 1927, *Desoulavy* 3583 (Akad. Lenin. ! type); Chernoruchenkov Mayak (lighthouse), Tachinchzhan (Tachunguan) mounts, southern Sikhota-Alin range, in oak-woods, 1936, *Kolesnikov* 283 (Akad. Lenin. ! K. !); near Milogradovo village, Olginski district, by the sea-coast on oak-covered slopes, 1930, *Schischkin* 1002 (Akad. Lenin. ! forma foliis 3- vel 7-foliolatis, foliolis fere inermis).

Of the nine specimens comprising these four gatherings, one only (*Desoulavy* 3583) is in flower and one only (*Desoulavy* 1049) in fruit, but vegetatively all agree closely. They diverge from *E. grandiflorum* in their usually trifoliolate leaves with more rounded, blunter, less spinous leaflets. The inner sepals, as shown by the two flowers seen, are broadest above the middle (instead of below, as in *E. grandiflorum*) and are bigger than those of any other *Epimedium*.

Subsectio II. ACERANTHUS.

Aceranthus Morr. & Dene, in Ann. Sci. Nat. Bot. ser. 2, II, p. 351 (1834).
Vindicta† Rafin. Fl. Tellur. II, p. 52, no. 187 (1837). *Epimedium* sect. *Aceranthus* Baill. Adansonia, II, p. 270 (1862), and Hist. Pl. III, p. 56 in adnot. (1871). *Epimedium* subgen. *Euepimedium* sect. *Phyllocaulon* series *Acerantha* Komarov in Acta Hort. Petrop. XXIX, p. 133 (1908), reimpr. in Fedde, Repert. Sp. Nov. VIII, p. 419 (1910).

Flowering stem normally bearing one leaf. *Leaves* normally 2-foliolate in one species, 3–5-foliolate in another. *Petals* spurless, flat, obovate. *Stamens* included.

This group consists of two (or three) species, one (or two) Japanese, the other Chinese.

Type-species:—*E. diphyllum* Lodd.

7. EPIMEDIUM DIPHYLLUM Loddiges. (Pl. 31, fig. 6.)

E. diphyllum Lodd., Bot. Cabinet, XIX, t. 1858* sine descript. (1832): Graham in Bot. Mag. LXII, t. 3448* (1835), and in Edinb. New Phil. Journ. XX, p. 191 (1835); Baker in Gard. Chron. N.S. XIII, p. 683 (1880): Franch. in Bull. Soc. Bot. France, XXXIII, p. 108 (1886): Ito in Journ. Linn. Soc., Bot. XXII, p. 432 (1887): Makino in Inuma, Somoku Dzus. ed. 3, II, t. 46 (1907): Komarov in Acta Hort. Petrop. XXIX, p. 133 (1908): Matsumura, Index Pl. Jap. II (Dicot.), p. 130 (1912). *Aceranthus diphyllus* Morr. & Dene, in Ann. Sci. Nat. Bot. ser. 2, II, p. 350, t. 14 (1834): Spach, Hist. Veg. Phan. VIII, p. 61 (1839): Wehrhahn, Gartenstauden, I, p. 452 (1930). *Vindicta begonifolia* Rafin. Fl. Tellur. II, p. 52 (1837). *E. grandiflorum* Marnock, Floricult. Mag. IV, p. 41, t. 40* (1839), non Morren. *E. japonicum* Sieb. ex Miq. Prolusio, p. 3 (1866), Ann. Mus. Lugd.-Batav. II, p. 71 pro syn. *Aceranthi diphyllyi* (1865), non Makino.

Figures.—Lodd., Bot. Cab. XIX, t. 1858*; Bot. Mag. t. 3448*; Ann. Sci. Nat. Bot. II, t. 14 (1834); Inuma, Somoku-Dzus. II, t. 46; Marnock, Floricult. Mag. IV, t. 40*; Baill. Hist. Pl. III, p. 56; Iwasaki, Honzo-Dzufu, VI, t. 12 recto; Useful Pl. Japan, III, t. 475* (1895).

'Herba gracilis, elegantissima; caulis subflexuosus. Folia gemina foliolis obliquis, laete-viridia integrerrima. Flores lactei, delicatuli Hab: in Japonia' (Morr. & Dene, loc. cit.).

Plant in flower 10–20 cm. high, rarely more. *Rhizome* short-creeping, caespitose, 1–2 mm. thick. *Leaves* basal and cauline, normally 2-foliolate

† Explained by Rafinesque as 'Epim. lat.', *Vindicta* (i.e. οινδικτα) is a name cited in various Dioscoridean codices (e.g. Codex Vindob., 106 recto) as the Roman equivalent of *Epimedium* Diosc. (i.e. ἐπιμήδιον), other synonyms being *Erineos*, *Thryas*, and *Polyrrhizon*; according to Wellmann, these names have probably been derived from a source other than the original text of Dioscorides, namely the περὶ βοτανῶν of the grammarian Pamphilos of Alexandria, compiled towards the end of the first century A.D. (cf. Singer, 1927, p. 24).

(? sometimes 3-foliolate with a small median leaflet or the two secondary petioles each 3-foliolate) ; *leaflets* ovate-deltoid or narrowly ovate, the tip blunt, the margin usually almost spineless, the base shallowly cordate and usually very unequal-sided, thin and membranous in texture, light green, sparingly pilose beneath, 2–5 cm. long, 1–2 cm. broad. *Flowering stem* bearing one normally 2-foliolate leaf ; *inflorescence* simple or the lower peduncle 2-flowered, almost glabrous, few-(4–9)flowered ; *pedicels* 1–2 cm. long. *Flowers* campanulate, pendulous, white, but pink forms (perhaps hybrids referable to $\times E. Youngianum \beta roseum$) are said to occur. *Outer sepals* oblong, blunt, 3 mm. long. *Inner sepals* narrowly ovate, bluntnish, horizontally spreading, 6 mm. long, 2·5 mm. broad. *Petals* slightly longer and broader than the inner sepals, obovate, rounded, flat, spurless but with a slight median furrow, 7 mm. long, 3–4 mm. broad. *Stamens* included, 3 mm. long : *anthers* nearly 2·5 mm. long.

Distribution.—South JAPAN :—Kyushu island, prov. Higo at Kiposan and Kumamoto, Maximowicz, Iter secund. 1863 (K. ! P. ! Calcutta ! Boiss. !) ; Shikoku island, prov. Tosa, Yasuda 1900 (Seattle !), at Ochi (U.S.N.H. 50822 !), Ochimura, J. Rein (B.!), and Sakawa (fide Matsumura, loc. cit.) ; Shikoku island, prov. Awa at Kutsusan (fide Matsumura, loc. cit.).

E. diphylum is a small species remarkable for its bifoliolate leaves and spurless white flowers, the generic name *Aceranthus* ('nom. genericum e vocabulis à sine, κέρας cornua et ἄνθος flos') referring to the latter and having no connexion with *Acer* (maple), although 'maple-wort' in Standardised Plant Names (1923), p. 4, has been seriously proposed as a popular name ! The Japanese 'Baikwa-ikariso' means 'peach-flowered *Epimedium*'. Messrs. Loddiges published no description, but their appropriate epithet was retained by later authors. According to Rein, it grows by the sides of paths through coniferous woods.

A curious specimen (Univ. Wien, Acq. No. 1780) collected by Watanabe (28 April 1896) at Ochi, prov. Tosa, differs from typical *E. diphylum* in having the stem-leaf composed of 4 binately arranged leaflets, while on the basal leaves one of the two secondary petioles may be bifoliolate and the other trifoliolate—as in some leaves of $\times E. Youngianum \gamma niveum$; the leaflets are almost spineless, the inflorescence 4–6-flowered, the flowers spurless and the ovary glabrous as in *E. diphylum*. The name *E. Musschianum* var. *trifoliolato-binatum* G. Koidzumi in Acta Phytotaxon., Kyoto, v, p. 126 (1936) †, is probably based on a similar plant from the same neighbourhood. Whether it presents a hybrid of *E. diphylum* \times *E. grandiflorum* (cf. $\times E. Youngianum$, p. 521) or *E. diphylum* \times *E. setosum* or an independent race, from the same stock as *E. diphylum*, in which, however, reduction of leaf from a biernate to a binary and ultimately bifoliolate type by suppression of the median leaflets has not reached so advanced and stable a state as in *E. diphylum* proper cannot be decided on present evidence.

† 'Var. *trifoliolato-binatum* Koidz. Caulis floriferus monophyllus foliis caulinis trifoliolato-binatis. Hab. Shikoku: prov. Tosa, prope Oppidum Kochi' (Koidz. loc. cit.).

8. *E. setosum* G. Koidzumi.

E. setosum G. Koidzumi in Acta Phytotaxonomica, Kyoto, 1, p. 19 (1932); Nemoto, Fl. Jap. Suppl. p. 236 (1936).

This plant is unknown to me, but according to Koidzumi's description, reproduced below, it would appear to differ from *E. diphyllum* in its paniculate, rarely simple inflorescence, biuncate basal leaves, setose-margined leaflets, and minutely puberulent ovary, the latter feature, if correct, being unique in the genus, while the others suggest the possibility of its being a natural hybrid between *E. diphyllum* and *E. grandiflorum* (which is recorded from Mizuta in Bitchu by Yoshino) similar to $\times E. Youngianum \gamma niveum$:

'*Epimedium (Aceranthus) setosum* Koidz., sp. n.

Epimedium diphyllum (non Lodd.) Yoshino, Fl. Bittsiuensis (1929), p. 33 †.

Rhizoma longum ad collum squatum. *Folia* radicalia palmatim biernata, in planta florifera nulla; *folia caulina* bifoliolata vel bi-binata; petiolis longis villosis ut in caule, apice ad articulationem praecipue dense villosis. *Caulis* solitarius erectus facie striatus villis mollis crispatis catenatis mox deciduisse villosus. *Foliola* longe petiolulata juniora tenuissima utrinque puberula, adulta pergamentacea fere glaberrima utrinque elevato-nervosa, subtus plus minus glaucina, profunde ovato-cordata acuta vel obtusa basi oblique sagittato-vel hastato-cordata in foliola lateralia, foliola terminalia basi auriculata vel sagittato-auriculata, margine setosa ad articulationes petioluli dense villosa. *Inflorescentia* anguste paniculata raro racemus simplex, oppositifolius, rhachide glabra ad nodum puberula; *pedicelli* bractea parva ovata scariosa basi suffulti glabri graciles, *flores* albi. *Petala* obovata apice rotundata *sepals* paulo longiora concava ecalcarata, stylo ovario minute puberulo aequilongo. Nom. Jap. Oh-baika-ikariso. *Distributio*.—JAPONIA, Chiugoku: Prov. Bittsiu [Bitchu], Bingo, Aki, Mimasaka' (Koidzumi, loc. cit.).

9. EPIMEDIUM PLATYPETALUM K. Meyer. (Pl. 25.)

E. platypetalum K. Meyer (!) in Limprecht, Bot. Reis. China. Ost-Tibets, in Fedde, Repert. Sp. Nov. Beih. XII, p. 380 (1922).

Plant in flower 18–30 cm. high. *Rhizome* long-creeping, very slender, 1–2 mm. thick. *Leaves* basal and caudate, 3- or 5-foliate, the petioles pilose with long reddish hairs forming conspicuous tufts at the nodes; *leaflets* broadly ovate to almost orbicular (about as broad as long), the tip rather rounded but acute, the margin very spinous, the base deeply cordate with the subequal lobes rounded and nearly touching, ultimately subcoriaceous in texture, papillose and sparingly pilose beneath, 1–3·2 cm. long, 1–2·5 cm. broad. *Flowering stem* bearing one (rarely two) 3- or 5-foliate leaf; *raceme* simple, very glandular, few-(6–8)flowered; *pedicels* 5–10 mm. long. *Flowers* small,

† Yoshino merely records *E. diphyllum* without description from Itani, Sayotani, and Kawase, all minor localities in Bitchu.

campanulate, probably white. *Outer sepals* broadly ovate, blunt, 2–3 mm. long. *Inner sepals* minute, triangular, reflexed, 1 mm. long. *Petals* (? oblong to) broadly obovate, rounded, flat, spurless, 8 mm. long, 5 mm. broad. *Stamens* included, 4 mm. long.

Distribution.—Western CHINA, prov. SZECHWAN, near Wentschwan-hsien, approx. $31^{\circ} 30' N.$, $103^{\circ} 30' E.$

This very distinct species is known only from the type-collection:—‘Ost-Tibet: Wen tschwan hsien, Hänge des Tung ling schan, 2600–2800 m.’ Limprecht 1386 (B. ! Univ. Wien ! Breslau!).

It may be recognized by its nearly orbicular coriaceous leaflets, its small growth, few-flowered inflorescence, and spurless flowers, and seems nearest to the Japanese *E. diphylum*.

Subsectio III. DIPHYLLON.

Epimedium subgen. *Euepimedium* sect. *Phyllocaulon* series *Diphyllon* Komarov in Acta Hort. Petrop. XXIX, p. 134 (1908).

‘Caule florifero diphyllo, foliis suboppositis’ (Kom. loc. cit.).

Flowering stem normally bearing two leaves, occasionally three or only one (*E. leptorrhizum*), usually opposite but occasionally alternate. *Leaves* 3-foliolate and coriaceous in most species, although 5-foliolate in *E. Davidi* and biteminate in *E. brevicornu* and occasionally in *E. sagittatum*.

This group occurs in China, with one species (*E. sagittatum*) apparently naturalized in Japan.

Standard species:—*E. sagittatum* (Sieb. & Zucc.) Maxim.

Series *Dolichocerae* †.

Flores magni vel medios; calcar petali subulatum, elongatum, usque ad 2·5 cm. longum, sepalo interiore longius.

Flowers large or medium-sized. Spurs of *petals* elongated and slender, up to 2·5 cm. long, exceeding the *inner sepals*.

Type-species:—*E. membranaceum* K. Meyer.

Subseries A.—Spurs of *petals* expanded from the base into distinct petaloid laminae c. 0·8–1·3 cm. deep, forming a cup enclosing the *stamens*.

10. *E. DAVIDI* Franchet.

This may possibly be regarded as consisting of two subspecies, of which the type may be provisionally distinguished as:—

Subsp. α .

E. Davidi Franch. (!) in Nouv. Archiv. Mus. Hist. Nat. Paris, ser. 2, VIII, p. 195, t. 6 (1885), reimpr. in Franch., Pl. David. II, p. 13, t. 6: Franch. in

† From δολιχός, long, κέρας, horn.

Bull. Soc. Bot. France, xxxiii, p. 109 (1886) : Voss, Vilmorin's Blumeng. p. 51 (1896) : Komarov in Acta Hort. Petrop. xxix, p. 138 p.p. (1908).

Figure.—Nouv. Archiv. Mus. Paris, ser. 2, viii, t. 6, vel Franch. Pl. David. II, t. 6.

Plant in flower 30–50 cm. high. *Rhizome* fairly long-creeping, 3 mm. thick. *Leaves* basal and caudine, 5- or 3-foliolate (the basal leaves abnormally 1-foliolate, the caudine leaves usually 3-foliolate), with tufts of reddish hairs at the nodes; *leaflets* narrowly to broadly ovate, the tip usually rounded and mucronate, the margin very spinous-serrate, the base deeply or shallowly cordate with the usually rounded lobes almost touching or diverging up to 150°, subcoriaceous, both sides distinctly reticulated with veins, beneath glaucescent, papillose and sparingly pubescent with short appressed hairs, usually less than 6 cm. long, 4·5 cm. broad. *Flowering stem* normally bearing two, opposite, 3- or 5-foliolate leaves, rarely alternate or three; *inflorescence* usually compound (with usually 3-flowered peduncles) below, simple above, loose, very glandular, 6–24-flowered; *pedicels* 1·5 cm. (in flower) to 3 cm. (in fruit) long. *Flowers* 2–3 cm. across, yellowish. *Outer sepals* blunt, ovate, 2–4 m. long. *Inner sepals* narrowly ovate, subacute, 4 mm. long, 1 mm. broad. *Petals* much longer than inner sepals, with distinct petaloid rounded laminae forming a cup 7–13 mm. deep and slender curved subulate spurs 1–1·5 cm. long. *Stamens* included, about 4 mm. long; *anthers* 3 mm. long. *Capsule* cylindric, comparatively long and slender, 2 cm. long.

Distribution.—Western CHINA, in mountain woods of west Szechwan province.

Type-locality.—‘In Thibeto orientali, ad montes lapidosos prope Moupine’ (Franchet, loc. cit.; 1886), approximately 31°–32° N. and 102° 50' E., north-east of Tatsienlu.

SZECHWAN:—Moupine, in shady woods, perennial plant with pretty yellow flowers, May 1869, *David* (P. ! type; K. ! L. !); Pao Hsing [=Mupin, fide Tang], 1600 m., under bushes, flower yellow, *Yü* 1892 (Fan Mem. I, Peiping ! Sci. Soc. Nanking!); west China, sine loc. sp., *Wilson*, Exp. Veitch. 3138† (K. ! B.M. !); Wenchuan Hsien, alt. 6000–8000 ft., woodlands, flowers yellow, *Wilson* Exp. Arn. Arb. 3788 (K. ! B. !); Han Yuan [=Hungya], 1500 m., in shade, fl. yellow, *Cheng* 668 (Sci. Soc. Nanking!); Tsaku lao, *Rosthorn*, 2597 (B. ! sine fl.); Mt. Omei, 1850 ; m., under woods, flowers yellow, *Yü* 387 (Fan M. I. Peiping !); Mt. Omei, forest, 1900 m., *Tü* 224 (Fan M. I. Peiping ! Sci. Soc. Nanking!); O-pien Hsien, 1800 m., under woods, corolla yellow, *Yü* 801 (Fan M. I. Peiping ! Sci. Soc. Nanking!), west of Kuan Hsien, 2340 m., flower light yellow, *Wang* 20851 (Fan M. I. Peiping !).

The specimens of Pratt from Tatsienlu (cf. *E. elongatum*) and of Henry from east Szechwan (cf. *E. membranaceum* β *orientale*) cited by Komarov under *E. Davidi* do not belong to this species.

† Wilson's entry for 3138 (Exp. Veitch) reads ‘Herb. 1½ ft. Fls. yellow. Rocks, Mt. West’ (fide Rehder, in litt.); it was probably collected in the neighbourhood of Mupin.

This species commemorates its first collector, the French naturalist and missionary, Jean Pierre Armand David (1826–1900).

Subsp. β .

Planta florens 40–65 cm. alta, foliolis anguste ovatis acuminatis usque ad 6·5 cm. longis, 3·5 cm. latis, ad *Epimedium hunanense* vergens sed foliis interdum 5-foliolatis, racemo glanduloso, floribus minoribus, etc., distincta.

Plant in flower 40–65 cm. high. *Rhizome* and basal leaves unknown. Cauline leaves 5- or 3-foliolate; leaflets narrowly ovate, the tip acuminate, the margin spinous-serrate, the base deeply cordate with the lobes diverging at 60°–90°, sparingly pubescent beneath, up to 6·5 cm. long, 3·5 cm. broad. *Flowering stem* bearing two opposite leaves; *inflorescence* simple, glandular, 15–20-flowered; *pedicels* ascending, to 3 cm. long. *Outer sepals* purple-tinged, the outer pair broadly ovate, the inner broadly obovate, blunt. *Inner sepals* ovate, subacute, ?3 mm. long, 2 mm. broad. *Petals* with rounded laminae 5 mm. deep and slender subulate spurs 1·5 cm. long.

SZECHWAN, reg. aust. : Hsiao-hsiang ling, 29° N., 103° E., in prato herboso, 7500–3000 m., *H. Smith* 1873 (Mus. bot. Uppsala !).

This may be only an extreme form of subsp. α , from which it diverges in its tall growth, more acuminate leaflets, and shallower petal-cup; the material available being young and incomplete, it seems best to describe the plant but leave it unnamed.

11. *E. HUNANENSE* (Hand.-Mazz.) Handel-Mazzetti. (Pl. 27.)

E. Davidii var. *hunanense* Hand.-Mazz. (!) in Anzeiger Akad. Math.-Nat. Wien, LXII (for 1925), no. 12, p. 131 (1926), reimpr. in Hand.-Mazz. Pl. Nov. Sinens. XXXIV, p. 4. *E. hunanense* (Hand.-Mazz.) Hand.-Mazz., Symbol. Sinicae, VII, Lief. 2, p. 324 (1931). *E. kunawarensis* S. Clay, Present-day Rock Gard. p. 209 (1937).

'Flores cum calcaribus 3½ cm. diam. Foliola ad 13×6 cm., annotina coriacea subtus glauca, juniora paululum pilosula, cetera planta glaberrima' (Hand.-Mazz. loc. cit.; 1926).

Plant in flower 40 cm. high. *Rhizome* short creeping, 3 mm. thick. *Leaves* basal and caudine, 3-foliolate; leaflets (of mature basal leaf) narrowly ovate, the tip acuminate, the margin very spinous-serrate, the base deeply cordate with the lobes tending to overlap, coriaceous in texture, beneath glaucous, papillose and sparingly pubescent or almost glabrous, 10–13 cm. long, 6 cm. broad. *Flowering stem* bearing two opposite 3-foliolate leaves; *inflorescence* compound with the lower peduncles 2- or 3-flowered, loose, almost glabrous, 10–16-flowered; *pedicels* 1–2 cm. long. *Flowers* 3·5 cm. across, yellow. *Outer sepals* oblong-elliptic, blunt, 4 mm. long, 2 mm. broad. *Inner sepals* broadly elliptic, blunt, 5–6 mm. long, 3–4 mm. broad. *Petals* much longer

than the inner sepals, with distinct petaloid rounded laminae forming a cup ± 8 mm. deep and fairly stout, nearly cylindric and horizontally spreading, blunt spurs 1.5–1.8 cm. long. *Stamens* 5 mm. long; anthers 4 mm. long.

Distribution.—CHINA, prov. Hunan, the species being at present known only from the type-gathering :—

HUNAN austro-occid., in monte Yün-schan prope urbem Wukang inter 400 et 1420 m. alt. s. m., substr. schisto argilloso; flores flavi, iv. 1919, Wang Te Hui, Pl. Sin. cur. H.-M. 43 (Bot. Instit. Univ. Wien ! V. !).

Subseries B.—Spurs of petals horn-shaped, with no distinct laminae.

12. E. ACUMINATUM Franchet.

E. acuminatum Franch. (!) in Bull. Soc. Bot. France, xxxiii, p. 109 (1886); Franch. Pl. Delavay. I, p. 40 (1889); Komarov in Acta Hort. Petrop. xxix, p. 138 p.p. (1908); Léveillé, Fl. Kouy-Tchéou, p. 48 (1915); Stearn in Journ. Bot. lxxi, p. 346 (1933).

E. sp. n., Komarov in Acta Hort. Petrop. xxix, p. 142 in obs. ross. (1908). *E. Komarovi* H. Léveillé (!) in Fedde, Repert. Sp. Nov. vii, p. 259 (1909), and Fl. Kouy-Tchéou, p. 48 (1915).

Plant in flower 25–50 cm. high. *Rhizome* sometimes long-creeping, 2–5 mm. thick. *Leaves* basal and caudate, 3-foliate; *leaflets* narrowly ovate to lanceolate, the tip long acuminate, the margin very spinous-serrate, the base deeply or shallowly cordate with the lobes rounded or acute, those of the lateral leaflets very unequal, thin and glabrous when young, coriaceous when mature with the lower surface glaucous, papillose and thickly or sparsely (sometimes almost glabrous) furnished with short appressed fairly stout unicellular bristles, 3–18 cm. long, 1.5–7 cm. broad. *Flowering stem* normally bearing two (abnormally three) trifoliolate opposite leaves; *inflorescence* compound with the lower peduncles 2–5-flowered, loose, glabrous or rarely sparsely glandular, few or many (10–55) flowered; *pedicels* 1–4 cm. long. *Flowers* 3–4 cm. across, yellow, white, rose-purple, or pale violet (according to collectors). *Outer sepals* blunt, the outer pair ovate-oblong, 3 mm. long, 2 mm. broad, the inner pair broadly obovate, 4.5 mm. long, 4 mm. broad. *Inner sepals* ovate-elliptic, acute, 8–12 mm. long, 3–7 mm. broad. *Petals* much longer than the inner sepals, horn-shaped, tapering from the swollen but lamina-less base, curving outwards, 1.5–2.5 cm. long. *Stamens* 3–4 mm. long; *anthers* 2.5 mm. long. *Capsule* cylindric, comparatively long and slender, about 2 cm. long (style included).

Distribution.—Western and central CHINA, i.e. provinces Kweichow, Yunnan, and Szechwan, in mountain woods between 1400 and 4000 m.

Type-localities.—*E. acuminatum*, ‘provincia Kouy-tchéou, unde habuit Dom. Perny’ (Franchet); *E. Komarovi*, ‘Kouy-Tchéou: Pin Fa, montagnes, mars 1908 (Jul. Cavalerie, 954)’ (H. Léveillé, loc. cit. 1909).

KWEICHOW (Kouy-Tchéou) province :—sine loc. sp., 1858, *Perny* (P. ! type); around Kouy-yang [=Kweiyang, lat. 26° 18' N., long. 106° 40' E.] in the mountains, among the rocks, beautiful rose-purple flowers, *Bodinier* 2146 (P. !); around Kouy-yang, wood of Kien-lin-chan; flowers rose, spurs purple, *Bodinier* 2146 D (P. !); Kwei-yang, near Mao-sha-tsin, flowers purplish white, *Teng* 90093 (Sun Yat. Univ. !), Pinfa [lat. 26° 3' N., long. 107° 8' E.], wood, flower pale violet, *Cavalerie & Fortunat* 954 (P. !); Pinfa, mountains, fls. whitish violet, *Cavalerie* 927 (K. !); Ganchouen [=Anshun, or Nganshunfu, southeast of Kweiyang], among rocks, *Cavalerie* 7857 (P. !. K. ! V. !); Anshun, flowers purple and white, *Teng* 0008 (Sun Yat. U. !).

YUNNAN :—Wood of Tehen-fong-chan [about 70 miles south of Soutchou], north Yunnan, at 1400 m., *Delavay* 2277 (P. !); Tehenfongchan, in the midst of rocks, fls. yellow, *Ducloux* 2121 (P. ! K. !), fls. white, *Ducloux* 2097 (P. !); Longki, damp rocks, fls. yellow, *Delavay* 4959 (P. ! Boiss. !).

SZECHWAN :—Nanchuan-hsien, alt. 5000-6000 ft., flower yellow, *Fang*, Fl. of Szechwan 802 (G. H. ! Fan M. I. Peiping ! K. ! P. ! U.S.N.H. !); Nanchuan, 1900 m., flower purple, *Tu* 3116 (Fan M. I. Peiping !); Nanchuan, under pine-forest, flower yellow-white, *Tu* 2763 (Fan M. I. Peiping !); Nanchuan, *Chii* 1305, 1057 (Fan M. I. Peiping !); Chinfu-shan, Nanchuan-hsien, *Chang* 233 (Sci. Soc. Nanking !); Mt. Omei, *Wilson*, Exp. Veitch 4729 (K. !); Mt. Omei, roadside, flower reddish, *Tu* 42 (Fan M. I. Peiping !), Mt. Omei, flower purplish white, *Yu* 312 (Fan M. I. Peiping !); Mt. Omei, 2000 m., flower yellow, *Wang* 23329 (Fan M. I. Peiping !); Mt. Omei, 1100 m., flower reddish, *Pong* 6108 (Fan M. I. Peiping !); among rocks between Jun-ezshin [Jung-hing-hsien] and Czin-ezi [Tsing-ki-hsien], *Potanin* (fide Komarov, loc. cit.); Ping-shan-hsien, 1000 m., among bushes, flower purple, *Tu* 5434 (Fan M. I. Peiping !).

From all species (except *E. sagittatum*) *E. acuminatum* may be distinguished by the closely-appressed short bristles which develop on the lower surface of the maturing leaflets; the young leaflets are glabrous. This remarkable feature is obvious in the type-material collected by Perny, but was unfortunately at first overlooked by Franchet, who mentioned in 1886 'son état tout à fait glabre' as distinguishing it from *E. Davidi*. Later Franchet noted it, remarking that 'les poils se développent très tardivement à la face inférieure des feuilles et ressemblent d'ailleurs à ceux de l'*E. sinense*' (1889); this observation has been overlooked, and the interpretation of the species caused much difficulty until Perny's material was examined. Franchet also described the leaves as 'bis ternatisecta, vel semel ternatisecta, vel haud raro tantum 6-foliolata', evidently mistaking a flower-stem, from which the inflorescence had broken away and left the two trifoliolate opposite leaves, for the remains of a biennial leaf. There are no perfect biennial leaves on the type of *E. acuminatum* or any other specimens examined; both caudate and basal leaves are always trifoliolate.

The narrowly ovate or lanceolate leaflets and the usually glabrous inflorescence are other diagnostic features. *E. sagittatum* (*E. sinense*), which it vegetatively much resembles, has smaller flowers of different structure. The large flowers of *E. acuminatum*, like those of *E. grandiflorum* and *E. membranaceum*, range from white and pale violet to rose and yellow, and the plant is worthy of cultivation. Léveillé's *E. Komarovii* collected by Cavalerie at Pinfa (E. !) is not distinct from *E. acuminatum* (Léveillé contrasted it with *E. sagittatum*), but a plant collected by Fius Ouen near Haytien (*Doucloux* 2354 in P. !) diverges from the type in its small leaflets and more slender rhizome $\pm 1\text{--}2$ mm. thick and may deserve varietal rank.

13. *E. MEMBRANACEUM* K. Meyer, sensu lato.

This species is closely allied to *E. acuminatum*, but differs in the slender spreading hairs of its leaflets. It may be divided into two subspecies, the first being the type :—

Subsp. α *GENUINUM* Stearn, nom. nov. (Pl. 27.)

E. membranaceum K. Meyer (!) in Limpricht, Bot. Reis. China. Ost-Tibets in Fedde, Repert. Sp. Nov. Beih. XII, p. 380 (1922) : Hand.-Mazz., Symbolae Sinicae, VII, Lief. 2, p. 324 (1931) : Stearn in Journ. Bot. LXXI, p. 346 (1933), sensu stricto. '*E. sagittatum* Baker, vel aff.', secundum auct. in Notes Roy. Bot. Gard. Edinb. XIV, p. 99, no. 19598 (1924) ; XVII, p. 26, no. 13888 (1929) ; XVII, p. 195, no. 16389 (1930), non (Sieb. & Zucc.) Maxim., necque Baker.

Plant in flower 20–60 cm. high. Rhizome long-creeping, 2–4 mm. thick. Leaves basal and cauline, 3-foliolate ; leaflets ovate or narrowly ovate or almost deltoid, the tip acute or short-acuminate, the margin very spinous-serrate, the base deeply or shallowly cordate with the lobes rounded or acute, those of the lateral leaflets rather unequal, thin when young and pubescent beneath, subcoriaceous when mature with the under side glaucous or very glaucous, papillose and pubescent with spreading slender multicellular hairs, 3–10 cm. long, 2–6 cm. broad. Flowering stem bearing two (abnormally three) trifoliolate opposite (abnormally alternate) leaves ; inflorescence compound with the lower peduncles usually 3-flowered, loose, glandular, few- or many-(5–35)-flowered ; pedicels 1–1.5 cm. long. Flowers 3–5 cm. across, pale yellow, white or pale rose (according to collectors). Outer sepals obovate, blunt, 4 mm. long, 2 mm. broad. Inner sepals ovate-elliptic, acute, 6–7 mm. long, 3 mm. broad. Petals much longer than the inner sepals, horn-shaped, tapering from the swollen but lamina-less base, curving outwards, 1.5–2.5 cm. long. Stamens 4 mm. long ; anthers 3 mm. long. Capsule comparatively long and slender, about 2 cm. long (style included).

Distribution.—Western CHINA, i.e. in west Szechwan and the adjoining region of north Yunnan.

In both places where collected by Handel-Mazzetti, this species grew sparsely on soft damp sandstone slopes covered by open scrub of *Andrachne*

lolonum Hand.-Mazz., *Rubus macilentus* Jacquem., *R. subtibetanus* Hand.-Mazz., *Deutzia longifolia* Franch., *Sorbus Folgeri* (C. K. Schn.) Rehder, *Ficus foveolata* Wall., *Morus australis* Poir., *Schizandra sphenanthera* Rehder et Wils., *Holboellia coriacea* Diels, and *Actinidia chinensis* Planch. and herbs such as *Tiarella polyphylla* D. Don, *Primula cyanocephala* I. B. Balf., and *P. werringtonensis* Forrest (cf. Journ. Roy. Hort. Soc. Hort. Soc. LIV, p. 55 ; 1929) ; Schneider found it on damp grassy slopes and Forrest on the margins of thickets and woods. Its average altitude is about 2200 m.

Type-locality.—‘Szetschwan, Kwanhsien, am Pass Yangtseling zwischen Yutschikou und Yinksiawan, 1300–1600 m.’ (K. Meyer), approx. lat. 31° N., long. 103° 30' E.

SZECHWAN :—Kwan-hsien at the Yangtseling pass between Yutschikou and Yinksiu-wan, 1300–1600 m., 16. iv. 1914, *Limprecht* 1293 (K. ! B. ! Univ. Wien ! Breslau ! type) ; Yin-hsiu-wan, 1200–1800 m., *Smith* 2402 (Uppsala !) ; 50 miles NW. of Chentu, Kuan-hsien Mts., Yingshawan, 5000 ft., *Fergusson* (K. !) ; on mt. Daliang-schan (Lolo Country) to the east of the town Ningyuen between Tjiaodjio and Lemoka, by a brook, alt. 2250 m. ; fls. pale yellow, *Handel-Mazzetti*, Iter Sinense 1597 (V. ! E. !) ; in the Loseschan mts. in thickets near the Wudadjing district, c. 2450 m. ; fls. sulphur, *Handel-Mazzetti*, Iter Sinense 1384 (V. ! Breslau !) ; between Ssuquehpa and Chaokio †, damp grassy slope, fls. yellow, *Schneider*, Iter Chinense 983 (B. ! K. ! Gen. !).

YUNNAN :—Yentchang region of Kiao Kia, *Ten* in *Ducloux* 1288 (E. !) ; Yunnansen, mountain to the north-east of the town ; fls. yellow, *Ducloux* 1287 (E. !) ; Wei Hsi valley, lat. 27° 20' N., alt. 7000 ft., margins of thickets ; plant of 12–18 inches, flowers white, *Forrest* 13888 (K. ! E. !) ; Mekong valley, lat. 28° N., alt. 6000–7000 ft., dry shady situations ; plant of 2–2½ ft., flowers flushed rose, *Forrest* 16389 (E. ! K. ! B. !) ; Mekong-Salwin divide, lat. 27° 54' N., long. 98° 50' E., alt. 8000 ft., margins of thickets and forests ; plant of 1½–2 ft., flowers pale yellow, *Forrest* 19598 (E. ! K. ! U.S.N.H. !) ; Shui-lu Shan west of Mei-hsi, lat. 27° 12' N., long. 99° 12' E., alt. 9000–10,000 ft., among scrub by streams ; plant of 2 ft., flowers yellow, *Forrest* 25471 (E. ! K. ! N.Y. ! U.S.N.H. !) ; mount Fu-chan, south-west of Wei-hsi, Mekong-Salwin divide, alt. 3700 m., in fir and spruce forest ; flower yellow, May–June, *Rock* 16973 (G.H. !).

Kurt Meyer distinguished *E. membranaceum* from *E. acuminatum* on account of the ‘glandular hairs of the pedicels, the yellow colour of the flowers, and the thin oval leaves’. These characters have proved of little worth, since yellow flowers and (occasionally) glandular pedicels occur in *E. acuminatum* and the leaflets of Meyer’s specimens of *E. membranaceum* are thin merely because they are immature, but the two species are distinct by reason of the differently-formed hairs on the lower surface of their leaflets.

Fide Schneider (in litt.), Chaokio and Tjiaodjio are the same place, 28° N., 102° 46' E.

Subsp. β ORIENTALE Stearn, subsp. nova.

Planta florens 20–50 cm alta. [Rhizoma 2·5 mm. crassum †.] Folia 3-folio-lata; foliola anguste ovata [vel lanceolata], acuminata, subter pilis gracilibus pubescentia, 5–6 cm. longa, 2·5–3·4 cm. lata in typo [verisimiliter 5–15 cm. longa, 2–5 cm. lata, demum subcoriacea]. Caulis florifer diphyllos, foliis oppositis; racemus simplex, glandulosa, 6–9-flora in typo [verisimiliter 5–22-flora]; pedicelli 1–2·5 [–? 5] cm. longi. Flores [parvi] usque ad 4 cm. diam. Sepala exteriora 4–5 mm. lata. Sepala interiora anguste ovata, acutiuscula, ± 8 mm. longa, 3–4 mm. lata. Petala cornuta, usque ad 2 cm. longa. Stamina 4–5 mm. longa: anthera 3–4 mm. longa.

Plant in flower 20–50 cm. high. Rhizome 2–5 mm. thick, apparently short-creeping. Leaves basal and caudine, 3-foliolate; leaflets narrowly ovate to lanceolate, the tip acute or short acuminate, the margin very spinous-serrate, the base deeply or shallowly cordate with the lobes rounded or acute, those of the lateral leaflets rather unequal, thin when young, subcoriaceous when mature with the under side glaucous, papillose and pubescent (principally along the veins and at insertion of the petiole) with spreading slender multicellular hairs, 5–15 cm. long, 2–5 cm. broad. Flowering stem bearing two trifoliolate opposite leaves; inflorescence simple, loose, flexuose, glandular, 5–22-flowered; pedicels 1–3·5 cm. long. Flowers up to 4 cm. across. Outer sepals blunt, 4–5 mm. long, 2–4 mm. broad. Inner sepals narrowly ovate, acute, 7–10 mm. long, 3–4 mm. broad. Petals much longer than the inner sepals, horn-shaped, tapering from the swollen base, up to 2 cm. long. Stamens 4–5 mm. long; anthers 3–4 mm. long.

Distribution.—Central CHINA, province Kiangsi and probably also in east Szechwan, Hupch, and Chekiang.

Type-locality.—Kiangsi province, Kiukiang ($29^{\circ} 44' N.$, $116^{\circ} 8' E.$).

KIANGSI:—Kiukiang, mountains, March to May, bright sulphur-coloured flowers, Miss F. M. Reid 11 (K. ! type, but lacking rhizome and mature leaves; enumerated by Komarov from ' Hin-kiang (prov. Guansi ?)' as ' *E. pubescens*'); Kew Kiang, Shearer (K. ! no flowers); Lushan, Maries (K. !); Chinkiang and Kiukiang, Maries (K. ! enumerated by Hemsley in Journ. Linn. Soc., Bot. xxiii, p. 32 (1886) as ' *E. macranthum*').

CHEKIANG:—sine loc. spec. Tsong 4279 (Manila !).

SZECHWAN, east:—Wushan, Henry 5526 (P. !), 5526 A (K. ! B. ! P. !).

HUPEH:—sine loc. sp., E. H. Wilson, Exp. Veitch 111 † (K. ! as

† The details in square brackets are from specimens other than the type.

‡ Prof. A. Rehder of the Arnold Arboretum informs me that the entry for no. 111 (Exp. Veitch) in Wilson's MSS. list is ' Herb. 1 ft. Fls. yellow large. Ichang etc.'; ' the word " etc." apparently indicates that part of no. 111 was collected elsewhere. Wilson unfortunately in his earlier collections sometimes placed plants collected in different localities under the same number (Rehder, in litt.). Under no. 111 two plants have been distributed:—one is *E. membranaceum* β *orientale*, to which Wilson's note ' 1 ft. fls. yellow' applies, and is therefore from Ichang: the other, *E. sutchuenense*, and presumably from another locality.

'*E. pubescens*'); Ichang, Henry 1251 (P. ! L. ! Boiss. ! as '*E. sagittatum*'); Patung, Henry 1434 (P. ! as '*E. macranthum*'); Kao-tien-chan (Kao-kien-sian), 800 m.s.m., Silvestri 720 (P. ! F. ! enumerated by Pampanini, Piant. Vasc. Silvest. Hupeh, p. 55 as '*E. pubescens*').

The material available of this plant is poor both in quantity and quality—even Reid 11, which has been selected as the type for want of a better one, lacks rhizome and mature foliage,—and the above description and distribution will probably require correction. I suspect it may prove specifically distinct from *E. membranaceum* & *genuinum*, from which it certainly diverges in its more eastern distribution, its proportionally narrower leaflets, and simple inflorescence. Specimens of this plant have previously been referred to *E. macranthum*, *E. sagittatum*, and *E. pubescens*.

14. *E. SUTCHUENENSE* Franchet. (Pl. 28.)

E. sutchuenense Franch. (!) in Morot, Journ. de Bot. VIII, p. 282 (1894); Komarov in Acta Hort. Petrop. XXIX, p. 138 (1908); Stearn in Journ. Bot. LXXI, p. 344 (1933).

Plant in flower 15–30 cm. high. Rhizome long-creeping, 1–3 mm. thick with internodes up to 13 cm. long. Leaves basal and caudate, 3-foliate; leaflets ovate or narrowly ovate, the tip abruptly long-acuminate, the margin very spinous-serrate, the base deeply cordate with the lobes rounded or acute and diverging at 30°–70°, coriaceous when mature, the under side glaucous, papillose and almost glabrous with only a few scattered grey hairs, 3–11 cm. long, 2–5 cm. broad. Flowering stem bearing two trifoliolate, opposite, equally developed leaves; inflorescence simple, glandular, few-(4–8)flowered; pedicels 1.5–2.5 cm. long. Flowers 3–4 cm. across, rose or mauve-purple. Outer sepals blunt, the outer pair ovate, 3 mm. long, the inner pair broadly obovate, 4 mm. long. Inner sepals narrowly lanceolate, long-acuminate, reflexing, 1.5–1.7 cm. long, 3 mm. broad near the base. Petals about as long as the inner sepals or slightly longer, horn-shaped, tapering from the swollen but lamina-less base, reflexing, 1.5–2 cm. long. Stamens protruding, 4–5 mm. long; anthers 3 mm. long.

Distribution.—Central CHINA, in mountain-woods of north-east Szechwan and west Hupeh provinces.

Type-locality.—‘ Su-tchuen oriental, dans les bois de Héou-pin, près de Tchen-kéou-tin’ (Franch. loc. cit.), approx. long. 109° E., lat. 32° N., and about 120 miles north-west of Hsing-shan-hsien, approximately 111° 10' E., 31° 20' N.

SZECHWAN :—in the woods of Héou-pin, near Tchen-kéou-tin, alt. 1600 m.; flowers rose, 28. iv. 1893, Farges 1272 (P. ! type).

HUPEH :—sine loc. spec. Wilson, Exp. Veitch 111 (N.Y. ! V. ! P. ! E. p.p. !)†;

† See p. 497, footnote.

Hsing-shan Hsien, abundant in woods ; flowers mauve-purple ; 4,000–7,500 ft., Wilson, Exp. Arnold Arb. 3787 (K. ! U.S.N.H. ! E. ! B. !).

E. sulchuenense was founded on Farges' no. 1272 in the Paris Museum, where it is represented by eight specimens, all much alike vegetatively, but only three possessing fairly well-preserved flowers. The specimens on the sheet bearing Farges' field-label have only shrivelled and immature flowers, of which it would be difficult to ascertain the structure, but from them apparently Franchet made his description, there being attached to this type-sheet a sketch of the flower which fits his description but is by no means accurate as regards the more mature flowers of the other specimens. He describes the petal as '6 mm. longo, sursum leviter curvato, sepalis fere dimidio breviore' and thus was led to exaggerate its affinity with *E. Fargesii* and to overlook its close connexion with *E. acuminatum*, from which it differs in its more slender and elongated rhizome, the hairs of the leaflets, and its longer sepals.

15. *E. LEPTORRHIZUM* Stearn. (Pl. 28.)

'*E. macranthum* Morr. & Dene', secundum H. Léveillé, Fl. Kouy-Tchéou, p. 48 (1915), non Morr. & Dene. *E. leptorrhizum* Stearn in Journ. Bot. LXXI, pp. 343, 346 (1933).

Plant in flower 12–30 cm. high. Rhizome long-creeping, 1–2 mm. thick, with internodes sometimes as much as 20 cm. long. Leaves basal and cauline, 3-foliolate, or abnormally 1-foliolate, the petioles furnished with spreading reddish hairs ; leaflets narrowly ovate, the tip long-acuminate, the margin very spinous-serrate, the base deeply cordate with the usually rounded lobes almost touching, those of the lateral leaflets very unequal, coriaceous when mature with the under side glaucous, papillose, and pubescent with scattered spreading or curled reddish hairs which are densest at the insertion of the petiolules and along the primary veins, 3–9·5 cm. long, 2–4·5 cm. broad. Flowering stem usually bearing one trifoliolate leaf with occasionally a rudimentary leaf densely clothed in reddish hairs arising opposite ; inflorescence simple, glandular, few-(4–8)flowered ; pedicels 1–2·5 cm. long. Flowers 4 cm. across, white tinged with rose or deep rose. Outer sepals blunt, ovate-oblong, 3–4 mm. long. Inner sepals narrowly elliptic or lanceolate, acute, 1·1–1·6 cm. long, 4–5 mm. broad. Petals longer than the inner sepals, horn-shaped, tapering from the swollen but lamina-less base, up to 2 cm. long. Stamens 4 mm. long ; anthers 3 mm. long.

Distribution.—Central CHINA, province Kweichow (Kouy-Tchéou) near the capital Kweiyang (Kouy-yang), approximately 26° 25' N., 106° 36' E.

Type-locality.—'Kweichow, environs de Kouy-yang' (Stearn, loc. cit.).

KWEICHOW : environs of Kouy-yang, wood of Kien-lin-chan ; only one leaf to the flowering stem ; flowers white lightly rose-coloured ; spurs grey on the inside, 14. iv. 1898, Bodinier 2184 (P. ! type ; Cantab. ! syntype) ;

environs of Kouy-yang, wood of the pagoda Lan-yo-chan ; flowers more or less deep rose, *Bodinier* 2184 Double (P. !) ; Ma-jo, Long-las-se, *Cavalerie* (K. ! specimen immature).

Of this species I have seen fourteen flowering specimens, one of which may be excluded from consideration as the stem-leaf has broken away. Eleven have each one trifoliolate and fully developed leaf below the inflorescence (the collector Bodinier even notes ' 1 seule feuille florale ' as characteristic) with no sign of other stem-leaves while two specimens have what appears to be a young second leaf thickly clothed in reddish hairs arising opposite the fully developed leaf ; in other details all agree. According to the classification proposed by Franchet these two should be placed in the group *Diphyllon*, with the species of which they have much in common ; the other specimens key out next to the Korean-Japanese species *E. grandiflorum* with which they have little real affinity and from which they differ conspicuously in their very slender rhizomes, constantly trifoliolate leaves with coriaceous leaflets, horn-shaped petals, etc. These features they share with *E. sutchuenense*, a Chinese species differing only in such minor details as degree of leaf-pubescentce and the acumination of the inner sepals, if the uniform development of its two stem-leaves is ignored. *E. sutchuenense* occurs in north-east Szechwan and Hupeh provinces, *E. leptorrhizum* in southern Kweichow. The two are thus distinct species, but their close resemblance in most respects and their almost adjacent areas suggest their differentiation from a common stock by isolation. They are of special interest in that *E. leptorrhizum*, by tending to lose one stem-leaf, varies in a character which has remained fairly constant in allied species and has thus come to be of taxonomic importance.

The Chinese name of this plant is ' Nu-ko-hwa ' (' ox-horn-flower ', fide C. C. Chang) rendered ' Mou-ko-hsa ' (' fleur à la corne de bœuf ') by Bodinier. Its scientific name, *leptorrhizum*, from $\lambda\epsilon\pi\tau\omega\mu\pi\zeta\sigma\varsigma$, ' with a thin, delicate root ', refers to its slender rhizome.

Series *Brachycerae* †.

Flores mediocres vel parvi ; calcar petali obtusum, breve, usque ad 7 mm. longum, sepalo interiore brevius.

Flowers medium-sized or small. Spurs of *petals* short, blunt, \pm 2–7 mm. long, shorter than the *inner sepals*.

Type-species :—*E. sagittatum* (S. & Z.) Maxim.

16. *E. BREVICORNUS* Maximowicz. (Pl. 29.)

E. brevicornu Maxim. (!) in Acta Hort. Petrop. xi, p. 42 (1890) : Komarov in Acta Hort. Petrop. xxix, p. 137 (1908). *E. rotundatum* Hao (!) in Fedde, Repert. Sp. Nov. xxxvi, p. 223 (1934), reimpr. in Contrib. Inst. Bot. Nat. Acad. Peiping, i, p. 3 (1935).

' *Florum forma colore et magnitudine aemulat E. pubescens*, a quo praeter

† $\beta\rho\alpha\chi\acute{\nu}\tau$, short, $\kappa\acute{\epsilon}\rho\alpha\varsigma$, horn.

cornua longiora aequa ac ab E. sagittato jam foliis binternatis differt' (Maxim. loc. cit.).

Plant in flower 20–60 cm. high. *Rhizome* short, clumped, 3 mm. thick. *Leaves* basal and caudine, usually binternate (9 leaflets), rarely 5- or 3-foliolate; *leaflets* ovate to broadly ovate, the tip acute or short-acuminate, the margin spinous-serrate, the base deeply cordate with the acute lobes of the lateral leaflets only slightly unequal, small and thin at flowering time, firm and parchment-like when mature with the under side almost glabrous, ±2 cm. long, 1·5 cm. broad at flowering time but later up to 8 cm. long, 6·5 cm. broad. *Flowering stem* bearing two opposite usually binternate leaves; *inflorescence* compound, loose, glandular, many-(20–50)flowered; *pedicels* 5–20 mm. long. *Flowers* 1·5 cm. across. *Outer sepals* narrowly ovate, dark, 1–3 mm. long. *Inner sepals* lanceolate, acute, white or yellowish, 10 mm. long, 4 mm. broad. *Petals* much shorter than the inner sepals, with very slight laminae and narrow, conical, blunt spurs 2–3 mm. long. *Stamens* exserted, 3–4 mm. long; *anthers* 2 mm. long. *Capsule* 1 cm. long.

Distribution.—Northern CHINA, extending across Kansu, Shensi, and Shansi provinces.

Type-locality :—‘Kansu: ad fl. Tao-ho, 11 Junii deflorescens; latere montium circa monasterium Dshoni, in fruticetis densis, 31 Maji fl.; ad fl. Tshiloku, 18 Junii 1885. defl. fr. fere maturi’ (Maxim. loc. cit.), these places being in the valley of the Tao river in east Kansu, approximately 25 miles north-west of Minchow, 34° 20' N., 104° 30' E.; Purdom and Rock have also collected it in this area. In Komarov’s revision *E. brevicornu* is recorded only from the type-locality.

KANSU :—about the monastery of Dshoni, 31. v. 1885, *Potanin* (L. ! type; B. ! E. ! K. ! V. !); Tao River basin, in river valley among scrub of *Berberis*, *Lonicera*, etc., on grassy slopes, alt. 8,000 ft.; flowers white, *Rock*, Arnold Arb. Exp. 12302 (N.Y. ! G.H. ! Fan M. I. Peiping ! Sun Yat. Univ. ! as ‘*E. pubescens*’); Minchow, 7,000–8,000 ft., *Purdom* (K. !); between Cheu-men and Cheu-tsaei-se, *Licent* 5278 (K. ! B.M. !); Sin-long-chan, near Lantcheou, *Licent* (K. ! B.M. ! P. !); Kar Ching Kou near Old Tao-chow, alt. 3100–3400 ft., forest, *Ching*, Pl. Kansu 941 (E. ! as *E. sagittatum*); Farrer’s ‘beautiful white *Epimedium* with flowers like small snowy butterflies aflutter loosely up the long spike’ found in the hills of southern Kansu (Eaves of World, I, p. 98; 1917) is probably *E. brevicornu*.

SHENSI :—Tapeishan, *Purdom* (K. !); Hancheng-hsien, *Purdom* (K. !); Lao-y-san, *Giraldi* (K. ! F. !); Huan-tou-san, *Giraldi* 2325, 7020 (B. ! F. !); Thui-kio-san, *Giraldi* 2323 (B. ! F. !); Lun san, *Giraldi* 2322 (B. ! F. !); Pao-ki, *Scallan* 67 (herb. *Biondi* in B. !); Pao-ki, Chifengsan, *Hugh* (= *Scallan*) 39 (B.M. !); Kusan, *Hugh* 206 (B.M. !); Miao-uan-san, *Hugh* (B.M. !); Fonscian-fu, *Scallan* 66 (herb. *Biondi* in B. ! F. !); mt. Tue-lian-pin, to the south-west of Si-ngan-fu, *Giraldi* 64 (herb. *Biondi* in B. ! F. !); Chung-nan-shan [=Tsin ling], 1,000 m., *Kung* 2469 (Sci. Soc. Nanking !).

SHANSI :—Chin Yuan-Wang, Chia Chuong, mountain valley in moist soil at 5,100 ft., *Ling* 1569 (Univ. Nanking, 9214 ! in herb. Calif. 263827 !); mountains, 1300 m., near Yu hiang hien and Hai tcheou, *Licent* 1886 (K. ! B.M.); Tongtingshan, Tapingti Setcheou, *Licent* 1398 (K. ! B.M. !); Tsin-yuan Hsien, alt. 1700 m., shaded slope, *Tang*, Shansi-Chili Exp. 1027 (N.Y. ! Sun Yat. Univ. ! Fan M. I., Peiping ! Sci. Soc. Nanking ! Univ. Nanking !); Yuan-chu distr., Shui-wang-ping, in subalpine woodland at about 2,100 m., *Smith* 6475 (Mus. Bot. Uppsala !); Yuan-chu-distr., Ye-cho-shan, at about 1,600 m., *Smith* 6470 (Uppsala !); Yung-chen, Chung-tiao-shan, in an open meadow at about 1,100 m., *Smith* 5945 (Uppsala !); Yuanchu distr., Yu-li Tzun, in open thickets at about 800 m., *Smith*, 6271 (Uppsala !).

HUPEH, north-central :—R. Pampanini, Pianta Vasc. Silvest. Hupeh, p. 55 (1911), ex Nuov. Giorn. Bot. Ital. xvii, p. 273 (1910), records *E. brevicornu* from Hupeh; but Silvestri's specimen (no. 719 from Ou-tan-scian), though lacking flowers (F. !), belongs to another species, probably *E. pubescens*, with 3-foliate leaves and ovate or narrowly ovate, acuminate leaflets finely pubescent beneath.

E. brevicornu may be readily distinguished from others of subsection *Diphyllon* by its biennial leaves with broadly ovate leaflets of firm but hardly coriaceous texture, especially in conjunction with its compound glandular inflorescence of small starry flowers with petal-spurs 3 mm. long. Flowers are lacking from much of the material enumerated above, which, however, agrees very well in its vegetative parts with typical *E. brevicornu*. Judging from the original description and a photograph of the type-specimen (*K. S. Hao* 468, collected in the Lanshan mountains near Wu-tu Hsien, south Kansu, about 102° E., 34° N.), *E. rotundatum* is merely a form with orbicular leaflets; it may be called *E. brevicornu* forma *rotundatum*.

17. *E. FARGESII* Franchet. (Fig. 14 on p. 457 and Pl. 29.)

E. Fargesii Franch. (!) in Morot, Journ. de Bot. VIII, p. 281 (1894) : Komarov in Acta Hort. Petrop. xxix, p. 137 (1908).

Plant in flower 20–40 cm. high. Rhizome probably short and clumped, 2–5 mm. thick. Leaves basal and caudate, 3-foliate; leaflets narrowly ovate, the tip acuminate, the margin very spinous-serrate, the base deeply cordate with usually acute lobes, those of the lateral leaflets unequal, coriaceous when mature with the under side white-glaucous, papillose, and glabrous or sparsely pilose, 4–10 cm. long, 1·5–3 cm. broad. Flowering stem normally bearing two (abnormally three, or absent) trifoliolate opposite leaves; inflorescence simple, or compound with the lower peduncles 3-flowered, loose, glandular, 7–15-flowered; pedicels 1·5–4 cm. long. Flowers ± 2 cm. long, with reflexing inner sepals. Outer sepals narrowly ovate, blunt, violet-tinged, 3–4 mm. long, 1·5 mm. broad. Inner sepals narrowly lanceolate, acuminate, soon reflexing, white, 1·5–1·8 cm. long, 4 mm. broad towards the base. Petals much shorter than the inner sepals, possibly dark violet when fresh, with slight bi-lipped

laminae and straight, cylindric-subulate, blunt spurs 7 mm. long. *Stamens* conspicuously protruding, 9 mm. long; *anthers* 3–4 mm. long. *Ovary* 1·3 cm. long.

Distribution.—North-central CHINA, province SZECHWAN. This very distinct species is known only from the type-specimens collected by *Farges* (no. 506 bis; P. ! K. !) in the mountainous region of Cheng-koutin ('Tchen-kéou-tin', approx. 32° N., 109° E.) in north-east Szechwan near the Shensi and Hupeh borders.

E. Fargesii is remarkable for its long narrow reflexing inner sepals and its long stamens; vegetatively it closely resembles *E. sutchuenense* which has much larger petals and shorter stamens; both inhabit the same region. It commemorates the French missionary and naturalist, Paul Guillaume *Farges* (1844–1912).

18. *E. PUBESCENS* Maximowicz, sensu lato.

This species differs from *E. sagittatum*, with which it has been confused, in its pubescence of slender spreading hairs and the relative proportion of the flower-parts, since its longer and more acuminate inner sepals distinctly exceed the outer sepals, petals, and stamens, while it is distinct from *E. Fargesii* in its shorter stamens, etc., and from *E. brevicornu* in its trifoliolate leaves, etc. Like *E. sagittatum* it may be divided into two subspecies differing in degree of leaflet-pubescent and in form of inflorescence.

Subsp. α PRIMARIUM Stearn, nom. nov.

E. pubescens Maxim. in Bull. Acad. Imp. Sci. St. Pétersb. xxix, p. 309 (1877); xxix, p. 222, t. 1 (1883), reimpr. in Mélanges Biol. St. Pétersb. ix, p. 712, & xi, p. 868: Franch. in Bull. Soc. Bot. France, xxxiii, p. 111 (1886): Maxim. in Acta Hort. Petrop. xi, p. 43 (1890): Komarov in Acta Hort. Petrop. xxix, p. 135 p.p. (1908), sensu stricto.

Figure.—Bull. Acad. Imp. Sci. St. Pétersb. xxix, t. 1 (1883).

'Foliis setoso-ciliatis subtus adpresso crebre pilosis, radicalibus simplicibus vel ternatis; caule simplici foliis 2 oppositis ternatis: foliolis cordato-ovatis longe acuminatis; racemo composito glanduloso-piloso; sepalis ovato-lanceolatis minutis patulis; filamentis ovario oblongo 5–9-ovulato aequalibus' (Maxim., loc. cit.; 1877).

Plant in flower 20–60 cm. high. *Rhizome* sometimes elongated, 3–4 mm. thick. *Leaves* basal and caudine, 3-foliolate (or the basal leaves sometimes 1-foliolate); *leaflets* ovate, narrowly ovate or lanceolate, the tip acuminate (abnormally rounded), the margin very spinous-serrate, the base deeply or shallowly cordate with usually rounded lobes, those of the lateral leaflets very unequal, coriaceous when mature, the under side persistently pubescent to tomentose with numerous fine multicellular spreading or curled grey hairs densest along the three primary veins and at the insertion of the petioles,

3–15 cm. long, 2–8 cm. broad. *Flowering stem* bearing two (abnormally three) opposite trifoliolate leaves; *inflorescence* compound, loose, usually glandular, many-(to 30)flowered, 10–20 cm. long, 5–6 cm. across towards base, with the lower peduncles 3–5-flowered: *pedicels* 1–2 cm. long. *Flowers* 1 cm. across. *Outer sepals* broadly ovate, purplish, 2–3 mm. long. *Inner sepals* lanceolate or narrowly lanceolate, acute or acuminate, white, several-nerved, 5–7 mm. long, 1·5–3·5 mm. broad. *Petals* minute, much shorter than the inner sepals, saccate, blunt, brownish, 2 mm. long, with no basal laminae. *Stamens* protruding, 4 mm. long: *anthers* 2 mm. long.

Distribution.—Northern, western, and central CHINA.

Type-locality :—‘ Prov. Schensi (Piasezki, 1875) ’ (Maxim., loc. cit.; 1817).

ANHWEI : Man choei ho, Courtois 3337 (Mus. Heude !).

SHENSI : near the river Hankiang among moist rocks, 3. iv. 1875, Piasezki (illistr. in Bull. Acad. Sci. St. Péterb. xxix, t. 1!); Nin-czan-czhou, Potanin (fide Komarov, loc. cit.) ; Shensi sud [ou Houpé orient.] Heude 90 (Mus. Heude ! hb. Stearn !).

SZECHWAN, west; without locality, Ward (Cantab. ! enumerated in Journ. Bot. li, p. 130; 1913, as ‘ *E. sagittatum* ’); along the Fukiang river north of Chongpa and Kiang yu, on mossy banks in company with 12015 [*Urophypha Rockii* Ulbrich, a small *Isopyrum*-like plant]; herb, flowers white, Rock 12016 (G.H. ! N.Y. ! enumerated in Journ. Arn. Arb. xiv, p. 14; 1933, as ‘ *E. brevicornu* ’); Kwan Hsien [30° 57' N., 103° 42' E.], wooded mountain slopes of Lao-djün-schan above the temple Erlwangmaio, 800 m., Limpricht 1249 (K. ! B. ! Breslau !); south of Kuan Hsien, 950 m., sepals dark purple, petals white, Wang 20373 (Fan M. I. Peiping !), Chin che Shan [about 10 miles south-west of Kuan hsien], Chien 5098 (Sci. Soc. Nanking !); Faber 472 (K. !) from Chung City in east Szechwan may belong here but lacks flowers.

A form—f. *lanatum* (‘ *E. pubescens* ’ Komarov, loc. cit. p. 136, quoad descript. ampl. e speciminibus szechuanensis Potanini in herb. L. ! foliolis subter conspicue arachnoideo-tomentosis)—remarkable for the dense ash-white cobwebby tomentum on the lower surface of the leaflets has been collected by G. N. Potanin in west Szechwan between Chengtu-fu and Yachou-fu (‘ between Pei-czshan and Ja-czshou, 27. iii. 1893 ’); the pedicels are glabrous, the outer sepals dark purple. Entangled among the rhizomes of this plant are various mosses, liverworts, *Selaginella* species, and a fern (*Onychium japonicum* (Thunb.) Kunze) indicative of a woodland habitat.

Subsp. β CAVALERIEI Stearn. (Pl. 29.)

E. pubescens var. *Cavaleriei* Stearn in Journ. Bot. lxxi, p. 345 (1933).

Plant in flower 40–60 cm. high. *Rhizome* apparently short, 5 mm. thick. *Leaves* 3-foliolate; *leaflets* narrowly ovate or lanceolate, the tip long-acuminate, the base shallowly cordate with usually rounded lobes, those of the lateral leaflets very oblique, coriaceous when mature, finely reticulated with veins above

and below, the lower surface sparsely pubescent with scattered slender hairs or subglabrous, 5–13 cm. long, 2–4·4 cm. long (possibly up to 25 cm. long, 6 cm. broad ; see below). *Flowering stem* bearing two (abnormally three) trifoliolate opposite leaves ; *inflorescence* compound, panicled and diffuse, glabrous, many-(about 60-)flowered, about 10–30 cm. long, towards the base up to 12 cm. across, with the spreading lower peduncles often 5–7-flowered ; *pedicels* 1–2·5 cm. long. *Flowers* 1 cm. across, with almost black *outer sepals*, white *inner sepals* 5 mm. long, minute *petals* 2 mm. long, *stamens* 3–4 mm. long, more or less as in *E. pubescens* α . *Capsule* 1 cm. long.

Distribution.—Central CHINA, prov. Kweichow (Kouy-Tchéou).

KWEICHOW : Ganchouen [=Anshun, south-west of Kwei-yang], bois, Cavalerie 7849 (K. ! type ; V. ! Sun Yat. Univ. ! Univ. Nanking !), 4251 (K. ! V. ! Univ. Nanking !), 8088 (K. !), 7166 (K. !); vicinity of Kuan-in-San, Anshun, in dense shade, flower white, Teng 0109 (Sun Yat. Univ. !).

In addition to the above the Kew herbarium contains two specimens without flowers collected by Cavalerie at Ganchouen, which apparently belong to this and represent its mature leaf-state. On one the leaflets (probably basal) are about 25 cm. long, 6 cm. broad, with the common petiole about 10 cm. or more long, the petiolules 5 to 8 cm. long. On the other the leaflets (certainly caudine) are 16 to 19 cm. long, 3 to 4 cm. broad. These huge leaflets are sparsely pubescent and distinctly papillose beneath.

A wide inflorescence and almost glabrous leaflets distinguish this subspecies, which comes very near *E. sagittatum* β *pyramidalis*. It is named after the French missionary and naturalist, Pierre Julien Cavalerie (b. 1869).

19. *E. SAGITTATUM* (Sieb. & Zucc.) Maximowicz, sensu lato.

This species is easily recognized by its two (rarely three) trifoliolate stem-leaves in conjunction with its compound inflorescence of minute flowers, differing from *E. pubescens* in the bristle-like hairs of the leaflets and the proportions of the perianth. The presence or absence of glands on the inflorescence is inconstant. It may be divided into two subspecies, α *typicum* being characterized by a fairly narrow, compact inflorescence :—

Subsp. α *TYPLICUM* Stearn, nom. nov.

Aceranthus sagittatus Siebold (!) & Zuccarini, Fl. Jap. fam. nat. Sect. prima, no. 296 ex Abhandl. Math.-Phys. Bay. Akad. München, IV, pt. 2, p. 175 (1845) ; Miq. Ann. Mus. Lugd. Batav. II, p. 71 (1865), reimpr. in Miq. Prolusio, p. 3 (1866), sensu stricto. *A. triphyllus* C. Koch (!) in Miq. Ann. Mus. Lugd.-Batav. I, p. 253 (1864). *A. pilosus* Schultes f. ex C. Koch, loc. cit. pro syn. *A. triphylli* (1864). *A. macrophyllus* Blume (!) ex C. Koch, loc. cit. (1864). *Epimedium sinense* Siebold (!) ex Miq. Ann. Mus. Lugd.-Bat. II, p. 71 (1865), reimpr. in Miq. Prolusio, p. 3, pro syn. *A. sagittati* (1866) : Franch. & Sav. Enum. Pl. Jap. I, p. 24, pro syn. (1873) : Hance in Journ. Bot. XX (n.s. XI)

p. 2 (1882) : Franch. in Bull. Soc. Bot. France, XXXIII, p. 110 (1886) : Ito in Journ. Linn. Soc., Bot. XXII, p. 432 (1887) : Komarov in Acta Hort. Petrop. XXIX, p. 134 (1908) : Wehrhahn, Gartenstauden, I, p. 453 excl. icones (1930). *E. Ikariso* Sieb. (!) ex Regel, Index Sem. Hort. Bot. Petrop. 1868, p. 89 (1868). *E. sagittatum* (Sieb. & Zucc.) Maxim. in Bull. Acad. Imp. Sci. St.-Pétersb. XXIII, p. 310 (1877), reimpr. in Mélanges Biol. St. Pétersb. IX, p. 713 (1877) : Baker in Gard. Chron. N.S. XIII, p. 683 (1880) : Makino in Iinumai, Somoku Dzus. ed. 3, II, p. 123, t. 44 (1907) : Hand.-Mazz., Symbol. Sinicae, VII, Lieff. 2, p. 325 (1931) : Terasaki, Nippon Shokub. Zufu, p. 153 (1933). *A. sagittifolius* Farrer, English Rock Gard. I, p. 8 (1919).

Figures.—Iinuma, Somoku Dzus. II, t. 44 ; Iwasaki, Honzo-Dzufu, VI, 9 verso, 10 recto * ; Terasaki, Nippon Shokub. Zufu, p. 153.

Plant in flower 25–50 cm. high. *Rhizome* short, nodose, 3–5 mm. thick. *Leaves* basal and caudate, 3-foliolate (the basal rarely biennial); *leaflets* narrowly ovate to lanceolate, the tip acute or acuminate, the margin very spinous, the base deeply or shallowly cordate, the terminal leaflet with equal rounded lobes, the lateral leaflets very oblique with the outer lobe large, deltoid and acute, the inner lobe smaller and rounded, coriaceous when mature, with the under side at first quite glabrous but usually becoming (as the leaflet expands and matures) sparsely or densely pilose with stout short unicellular appressed hairs, very variable in size, often 5 cm. long, 3 cm. broad, but sometimes up to 19 cm. long, 8 cm. broad. *Flowering stem* bearing two (abnormally three) opposite trifoliate leaves; *inflorescence* compound, usually glabrous, many-(20–60)-flowered, oblong and comparatively narrow in outline, 10–20 (rarely 30) cm. long, 2–4 cm. across, with the lower peduncles 3-flowered; *pedicels* 1 cm. long. *Flowers* 8 mm. or less across. *Outer sepals* blunt, purple-spotted, the outer pair narrowly ovate, 3.5 mm. long, 1.5 mm. broad, the inner pair oblong-ovate, 4.5 mm. long, 2 mm. broad. *Inner sepals* ovate-deltoid, acute, white, 4 mm. long, 2 mm. broad. *Petals* minute, almost as long as the inner sepals, saccate, blunt, brownish-yellow, with slight lateral flanges at base, 2–4 mm. long. *Stamens* protruding, 5 mm. long; *anthers* 3 mm. long. *Capsule* 1 cm. long.

Distribution.—Mountains of central CHINA ; apparently naturalized in Japan where it has long been cultivated. According to Handel-Mazzetti (in litt.) *E. sagittatum* is a scarce plant in nature ; he found it growing sparsely under rock boulders on steep sunny slopes covered with open scrub of *Prunus Simonii* Carr., *Spiraea chinensis* Maxim., *Loropetalum chinense* (R. Br.) Oliver, *Rhododendron Simsii* Planch., etc.

Type-locality.—Japan, probably cultivated (see below).

CHINA :—

CHEKIANG :—Ningpo Mounts, Tientai, 3,000 ft., Faber (B. ! P. !) ; Tihtaishan, Tih-tai, 600–1,200 m., Ching 1493 (B. ! E. ! K. ! Sci. Soc. Nanking !) ; without exact locality, Barchet 21 (U.S.N.H. !).

FUKIEN :—Foochow, *Carles* (E. !); Inghok Hsien, Tang Quang Yen, in shade under rocks, *Chung* 2637 (B. ! K. !), *Chung* 1359 (B. ! K. ! V. ! Fan M. I. Peiping ! Sun Yat. U. ! Univ. Nanking !), *Chung* 3187 (Sun Yat. U. !).

KWANGTUNG :—Ju-yuan Hsien [= Yung yü], *Ko* 54112 (Sun Yat. U. !).

KIANGSI :—Kui Chi Hsien, on open hillside, 2800 ft., *Hu* 1431 (B. ! Manila !).

HUNAN :—near the town Tschangschia, among rocks on mt. Guschau, alt. 250 m.; sepals rose, petals white, anthers green, *Handel-Mazzetti* 11629 (V. ! E. ! K. !).

HUPEH :—near Ichang, *Watters* 21114 in herb. Hance (B.M. ! an immature specimen, perhaps of subsp. β).

ANHWEI (Ngan-hoei, Anhui) :—Tongmen, *Courtois* 25488 (Mus. Heude !); Chanken, near Wu-yuen, *Courtois* 28558 (Mus. Heude !); Hieou-ning, *Courtois* 25223 (P. ! Mus. Heude !), 27217 (Mus. Heude !); Ye-tsien-se, *Courtois* 27117 (Mus. Heude !); cf. map in Belval, Fl. Ngan-hoei (1933).

FORMOSA (Taiwan) :—Although an ‘*Epimedium* sp.’ without flowers is described from Formosa by Matsumura and Hayata (Journ. Coll. Sci. Tokyo, xxii, pp. 18–19; 1906) and *E. sagittatum* is recorded in Matsumura, Index Pl. Jap. II (Dicot.) p. 130 (1912), I have seen no material from Formosa, and Dr. Genkei Masanume (in litt., 1934) of Taihoku Imperial University, Formosa, states that the occurrence of an *Epimedium* on the island is very doubtful.

Epimedium sagittatum was originally made known as a Japanese plant, probably from cultivated material, as it has long been grown in Japan for its distinct foliage and supposed medicinal properties; its introduction from China is said to be recorded in old Japanese literature, and modern Japanese authorities, e.g. Makino and Nemoto (1931), do not regard it as indigenous. The leaflets are very variable in form, size, and hairiness; cultivated specimens not otherwise distinguishable may have the leaflets ‘*glabra*’ as described by Zuccarini or ‘*subtus pilis brevissimis adpressis laxe vestita*’ as described by Regel, these hairs often developing as the leaflets mature; similar variation occurs in wild material. After flowering the leaflets sometimes enlarge considerably; *Aceranthus macrophyllus* (‘*foliola . . . 7 poll. longa et supra basin 3 poll. lata et latiora*’, Koch, loc. cit.; specim. authent. in herb. Leiden !) was founded on this mature state. The type-sheet (herb. Leiden, no. 898, 196–203) of Koch’s other species, *A. triphyllum*, consists of fragmentary leaves of *E. grandiflorum* and a depauperate flowering specimen of *E. sagittatum* with one stem-leaf broken away. The Leiden Rijks Herbarium contains also numerous specimens from Japan labelled *A. macrophyllus* by Blume and *E. Ikariso* or *E. sinense* by von Siebold (with a diagnosis:—‘*Epimedium sinense* Siebold. Nectariis 4 petaloideis erectis apice fovea nectarifera, floribus paniculatis, foliis binternatis, foliolis serrato-ciliatis dimidiato cordato-hastatis medio hastato’). The plant was formerly grown in European botanic gardens (to which it was introduced by Siebold shortly before 1856 and from which it has now almost disappeared) as *E. Ikariso* (Boiss. ! B. !), but since ‘*Ikariso*’

is merely the Japanese vernacular name for *E. grandiflorum* (cf. p. 483) it is also applied horticulturally to forms of the latter. The Japanese name of *E. sagittatum* is 'Hozakino-ikariso', i.e. anchor-plant with compound inflorescence.

Professor H. H. Hu of Peking informs me that this species is mentioned in Chinese herbals as an aphrodisiac—for sheep! The description of the 'Yin-yang-huo' given by Li Shi-chen (16th cent.) and other herbals translated by Bretschneider, *Botanicon Sinicum*, III, p. 55 (1896) fits *E. sagittatum*: both rhizome and leaves are stated in the Emperor Shen-nung's herbal *Pen ts'ao king* (c. B.C. 202 to A.D. 221) to be officinal, pungent in taste, but not poisonous. According to D. Hooper ('On Chinese medicine' in *Gardens' Bull.*, Straits Settl. VI, p. 58; 1929) in Malaya the leaves are reputed tonic, stimulant, and antirheumatic and useful in kidney troubles, while G. A. Stuart, *Chinese Materia Medica*, p. 4 (1911), says that 'in decoction it is used in corneal affections and ulcerations of the eye after exanthematous diseases' and that it is 'prescribed in sterility and barrenness, and is said to have great virtues in these conditions'. This reputation of the Asiatic *E. sagittatum* contrasts with that of the European *E. alpinum* or 'Barrenwort', formerly supposed to be 'an enimie to conception' (Gerard, 1597). The name 'Ying-yang-huo' (herb causing goats to copulate excessively), corrupted by Chinese druggists in Malaya into 'Yim-yong-kok', is, according to T. Ishidoya, *Chinesische Drogen*, p. 35 et seq., figs. 44–47 (1933), applied to the dried summer leaves of four plants serving 'als tonisches Mittel gegen Niere', namely, *E. sagittatum* in Shanghai (cf. op. cit. fig. 45), but *E. grandiflorum* (op. cit. fig. 44) in Manchuria, and *Thalictrum tuberiferum* and *Astilbe chinense* in Taiko, Formosa. Another Chinese name is 'Hsien-ling-pi'.

Subsp. β PYRAMIDALE (Franch.) Stearn.

E. sinense var. *pyramidalis* Franch. Pl. Delavay, I, p. 40 (1889): Komarov in *Acta Hort. Petrop.* XXIX, p. 142 in obs. Ross. (1908). *E. sagittatum* var. *pyramidalis* (Franch.) Stearn in *Journ. Bot.* LXXI, p. 346 in adnot. (1933).

'Inflorescentia pyramidalis, ramis inferioribus et mediis binternatim divis' (Franch. loc. cit.).

Plant in flower 35–68 cm. high. Inflorescence compound, glabrous, or glandular, many-(50–95)flowered, forming a loose panicle of somewhat pyramidal outline, 20–37 cm. long, 8–12 cm. across (sometimes less) towards the base, with the lower peduncles 3–5-flowered and outspread; pedicels 5–15 mm. long. Flowers 8 mm. across, as in subsp. α , with purplish blunt outer sepals, hyaline ovate inner sepals 4 mm. long, minute saccate petals, and slightly exserted stamens 5 mm. long.

Distribution.—Central CHINA, apparently more northern and limited in area than subsp. α , occurring in east Szechwan and west Hupeh. Franchet gives

the type-locality as 'Yunnan, ad Tchong-tcheou prope Kouï-fou, secus Yang-tche-kiang', but the type is dated '31, March 1882' and, according to Bretschneider's account of Delavay's travels (*Hist. Europ. Bot. Discov. China*, II, p. 875), must have been collected in east Szechwan near the Hupeh border on the bank of the Yangtse-kiang or Blue River not far from the town of Kuichoufu, approximately 31° N., 109° 31' E., when Delavay was travelling upriver to Yunnan and not in Yunnan itself.

SZECHWAN :—au bord du Fleuve Bleu (rive droite) à Tchongtcheou près de Kouifou, 31. iii. 1882, *J. M. Delavay* (P. ! typus; forma pedicellis glabris); Iron-mountain, Suiting-fu, on ravine, in shady and moist place, occasional, *Fang* 10247 (*Sci. Soc. Nanking* ! forma pedicellis glandulosis).

HUPEH :—Changyang, by roadside; flowers white, *Wilson*, Exp. Veitch, 71, 71 a (V. ! B. ! K. ! N.Y. ! P. ! forma pedicellis glandulosis).

Referring to specimens examined at Paris, Komarov says:—"I also saw there two specimens of *E. sinense* var. *pyramidalis* Franch. of which the description is unknown to me; this variety is characterized by a pyramidal inflorescence much outspread in its lower part and 40 cm. long, the flowers very small as in typical *E. sinense*. It is possible this may be a distinct species" (Komarov, loc. cit. in obs. Ross.).

Subsectio IV. POLYPHYLLON.

Epimedium subgen. *Euepimedium* sect. *Phyllocaulon* series *Polyphylla* Komarov in *Acta Hort. Petrop.* XXIX, p. 139 (1908).

'Caule florifero polyphyllo, foliis alternis' (Komarov, loc. cit.).

Flowering stem bearing several (1-8) alternate leaves, with numerous thin, ovate to nearly orbicular leaflets.

Of this group, one species (*E. elatum*) occurs in India, the other (*E. elongatum*) in China.

Type-species:—*E. elatum* Morr. & Dcne.

Series *Elongatae*.

Inflorescentia angusta, saepe simplex. Flores mediocres, 2-3 cm. diam.; calcar petali elongatum, c. 1.3 cm. longum, sepalo interiore longius.

Inflorescence narrow, often simple; *flowers* medium-sized, 2-3 cm. across. Spurs of *petals* elongated and slender, about 1.3 cm. long, exceeding the *inner sepals*.

20. EPIMEDIUM ELONGATUM Komarov. (Pl. 30.)

E. elongatum Komarov (!) in *Acta Hort. Petrop.* XXIX, p. 140, t. 3 (1908), reimpr. in Fedde, *Repert. Sp. Nov.* VIII, p. 419 (1910). '*E. Davidi* Franchet' Komarov, op. cit. p. 138 p.p. quoad spec. *Prattii* (1908), non Franch.

Figure.—*Acta Hort. Petrop.* XXIX, t. 3.

' Ab affini *E. elato* M. D. calcare elongato incurvo gracili, quam petala [sepala interiora] triplo longiore, racemo angusto, antheris brevioribus bene differt ' (Komarov, loc. cit.).

Plant in flower 25–60 cm. high. *Rhizome* moderately long-creeping, 2–4 mm. thick. *Leaves* basal and caudine, tri- or biernate, rarely 3-foliolate; *leaflets* ovate to sub-orbicular, the tip rounded and apiculate to short-acuminate, the margin spinous-serrate, the base deeply cordate with the usually subequal lobes rounded or acute, thin and papery in texture, glabrous or with a few scattered hairs beneath, both sides finely reticulated with veins, 1·5–7·3 cm. long, 1–6 cm. broad. *Flowering stem* usually bearing three, less often two or one, irregularly spaced (5 mm. to 9 cm. apart) alternate or rarely opposite leaves, the lower tri- or biernate, the upper biernate or 3-foliolate; *inflorescence* simple or compound with the lower peduncles 3–5-flowered, sparsely glandular, many-(17–30)flowered, elongated, 15–30 cm. long, 4–8 cm. across; *pedicels* appressed or spreading, 1–2 cm. (in flower) to 3 cm. (in fruit) long. *Flowers* 2·5–3 cm. across. *Outer sepals* ovate, blunt, whitish, 3–4 mm. long, 2 mm. broad. *Inner sepals* lanceolate, acute, purple, 4 mm. long, 1·5 mm. broad. *Petals* longer than the inner sepals, tapering from their swollen but lamina-less bases into slender horizontally spreading or curved spurs 1·5 cm. long. *Stamens* slightly protruding, 3 mm. long; *anthers* 2 mm. long. *Capsule* elongated and slender, 2 cm. long.

Distribution.—Western CHINA, in mountains on the Chwanpien-west Szechwan border, near Tatsienlu (Tachienlu, Dadsianlu), approximately 30° N., 102° E.

In herbaria two forms of this species are represented, but as the differences are probably due to environment they are distinguished here but not given names:—

E. elongatum forma α (habitu elata, foliolis magnis subglabris).

No type-locality nor collector is given in Komarov's description, but authentic material (L. ! K. !) matching the original description and plate bears the following label in Komarov's handwriting:—' Tibet, Kam, 1893, in valle Pa-syn-kou supra pagum Dshusme, sinice Mo-nju, G. N. Potanin, 19. vii. 1893'. According to Bretschneider's account (1898) of Potanin's travels, the type must therefore have been collected in north-west Chwanpien or north-west Szechwan, erroneously called 'Kam' on Potanin's labels, while descending the Daboshan mountains (approx. 31° N., 102° E.) about 40 miles north of Tatsienlu.

Sikang, north of Tachienlu, 2800 m., fl. yellow, herb. 1·5 ft. tall, Cheng, 1468 (Sci. Soc. Nanking!).

E. elongatum forma β (habitu minore, foliolis parvis subter sparse pilosis). W. Szechwan and Tibetan border, near Tachienlu, between 9,000–13,500 ft., Pratt 168 as '*E. Davidi*' (K. ! B.M. ! Calcutta !); Baurong to Tachienlu, via Hadjaha, 9,000–15,500 ft., Stevens 196, 251 (B. ! Field Mus. Chicago !).

This Chinese species is like the Indian *E. elatum* in habit, but quite distinct in floral and other characters (cf. p. 513). When the flower-stem bears only two leaves at almost the same level, it is more like species of *Diphyllon* series *Dolichocerae*, though easily distinguished from *E. Davidi* by its lamina-less petals and from *E. acuminatum* and allies by its numerous papery leaflets.

Regarding its habitat, Herbert Stevens writes that his specimens were collected 'between Wushi (12,000 ft.) and Zamba Ku (11,600 ft.) or Hadja Tungu (13,000 ft.). I passed through numerous delightfully wooded valleys, between 12,000–13,000 ft. and rich with shrubs and flowers. These are within 29–30° N., 101–102° E. There is rainfall and temperature similar to that in this country [England], but these valleys are sheltered'.

Series *Elatae*.

Epimedium sect. *Microceras* Morr. & Dene in Ann. Sci. Nat. Bot. ser. 2, II, p. 349, p.p. min. (1834).

Inflorescentia diffusa, ramosa, multiflora. Flores parvi, vix 1 cm. diam.; calcar petali breve, circa 3 mm. longum, sepalo interiore brevius.

21. *E. ELATUM* Morren & Decaisne. (Fig. 1, on p. 416.)

E. elatum Morr. & Dene (!) in Ann. Sci. Nat. Bot. ser. 2, II, p. 356 (1834) : Dene in Jacquemont, Voyage dans l'Inde, IV (Bot.), p. 9, t. 8 (1844) : Seringe, Fl. Jardins, III, p. 274 (1849) ; Hook. f. & Thoms., Fl. Ind. p. 231 (1855) : Hook. f., Fl. Brit. Ind. I, p. 112 (1872) : Baker in Gard. Chron. N.S. XIII, p. 620 (1880) : Franch. in Bull. Soc. Bot. France, XXXIII, p. 111 (1886) : Komarov in Acta Hort. Petrop. XXIX, p. 139 (1908) : Wehrhahn, Gartenstauden, I, p. 453 (1930). *E. hydaspidis* Falconer in Proc. Linn. Soc. I, p. 18 (1839), nomen subnudum †.

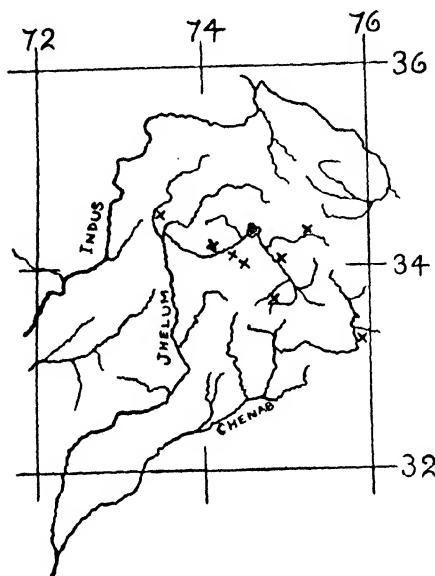
Figure.—Jacquemont, Voy. Bot. t. 8.

Plant in flower 50–140 cm. high. *Rhizome* moderately short, nodose, 3–5 mm. thick. *Leaves* basal and caudine, ternately compound, the larger leaves with 50 or more leaflets ; *leaflets* ovate or broadly ovate, the tip rounded but apiculate, the margin spinous-serrate, the base deeply or shallowly cordate, with the lobes usually subequal and rounded, thin and papery in texture, sparingly pilose beneath, with a few hairs near the veins or ultimately glabrous, very variable in size, 2–6 cm. long, 1.5–4.5 cm. broad. *Flowering stem* tall, ribbed towards the base, bearing 3–8 irregularly-spaced alternate leaves, the lower leaves large, the others smaller, those immediately below the inflorescence being reduced to 5 or 3 (or even 1) leaflets ; *inflorescence* compound, glabrous or glandular, many-(50–100)flowered, usually very diffuse, 20–30 cm. long, 15–25 cm. across, the lower branches subtended by small 5-,

† 'Cashmeer I have also a new *Epimedium*, a large handsome leaved herb, *E. hydaspidis* (mihi)' (Falconer, loc. cit.). The river Hydaspes of classical geographers, e.g. Mela and Strabo, is now the Jhelum, a tributary of the Indus which flows through Kashmir ; cf. W. Smith, Dict. Greek & Roman Geogr. I, p. 1100 (1873).

3- or 1-foliolate leaves or large cuneate-based lanceolate spinous-margined green bracts; *pedicels* filiform, 5–20 mm. long. *Flowers* scarcely 1 cm. across. *Outer sepals* ovate, blunt, whitish, 1–2 mm. long. *Inner sepals* narrowly ovate, acute, hyaline or yellowish, soon reflexing, 5 mm. long, 2·5 mm. broad. *Petals* shorter than the inner sepals, slipper-like, cylindric, blunt, 2–3 mm. long, with no basal laminae. *Stamens* protruding, 5 mm. long; *anthers* purplish, 1·5 mm. long. *Capsules* comparatively short and stout, 1 cm. long.

Distribution.—North-west Himalaya, not known outside Kashmir, north-west British India.



MAP no. 6.—The places in the north-western Himalaya in and about the vale of Kashmir where *Epimedium elatum* occurs.

Type-locality.—‘Frequens in montibus Cachemiricis circa Choupienna et Hirpour’ (Morren & Decaisne, loc. cit.), i.e. to the west of Shupiyan ($33^{\circ} 43'$ E., $74^{\circ} 50'$ N.) near Hirpur, where Victor Jacquemont (1801–32) discovered it in June 1831 at about 7500 ft. (cf. Jacquemont, Voy. III, p. 221; 1841).

According to B. O. Coventry (in litt.), *E. elatum* is found in mountain-woods, usually at 8000 ft., but ranging between 4500 and 9000 ft., throughout the upper valleys of the Chenab and the Jhelum, with its tributaries the Sind, Kishenganga and Kurhai rivers (but not in the Indus valley). It is rather local and grows in deep moist humus soils, forming small patches here and there, usually beneath silver firs (*Abies* sp.). Apparently only a few flowers produce capsules. The climate of Kashmir is temperate, somewhat like that of England but with greater extremes, e.g. a severe winter with all country.

above 7000 ft. under deep snow for several months, a mild spring and autumn, and a warmer and damper summer.

KASHMIR :—Chenab, 6000 ft., *Thomson* (K. !); Kishtwar, 6–8000 ft., *Thomson* in Herb. Ind. Hook. f. & Thoms. (K. ! B. ! Cantab. ! E. ! P. ! Copenhagen ! F. !); in the lower woods about Hirpour, *Jacquemont* 698 (K. !), 575 (P. !); 459 (P. !), Hirpour, c. 8000 ft., *Clarke* 2866 (K. ! Calcutta !); mount behind Srinagar, 7–8000 ft., *Stewart* 4140½ (K. !); Gulmarg [Gulmarg], common in woods, *Aitchison* 3 (K. !); Baramula pass, 4500 ft., *Winterbottom* 7849 (K. !); Sind valley, 8000 ft., *Clarke* 30959 (K. !); Sonamarg, 9–10,000 ft., *Stewart* (N.Y. !); Kishenganga, *Meebold* 3166 (B. ! Breslau !); in mixed woods, c. 8000 ft., above Gora in the Kishenganga valley, *Drummond* 15009 (K. ! E. !); Kagan valley, 4–7000 ft., *Stewart* 512 (Calcutta !); Bonj, Kagan valley, district of Hazara, *Duthie* 21115 (K. ! Calcutta !), 19133 (K. !); Limbar Nullah, 7–8000 ft., *Duthie* 11141 (E. !); near Muliyal, *Winterbottom* 3164 (K. !); without definite locality, *Falconer* in Herb. E. Ind. Co. 104 (K. ! B. ! Cantab. ! Calcutta ! Copenhagen !).

E. elatum is a remarkably tall species with the general habit of a *Thalictrum*, easily recognized by its numerous papery leaflets, its several-leaved flowering stem and its large loose panicle of tiny flowers. It has no close ally. *E. elongatum* of west China agrees in having usually several alternate stem-leaves with numerous thin leaflets, but differs in its more slender elongated rhizome, dwarfer habit, often simple inflorescence, larger flowers with long-spurred petals, shorter stamens and elongated slender capsules, and thus approaches the subsect. *Diphyllon* series *Dolichocerae*. *E. elatum*, on the other hand, suggests subsect. *Diphyllon* series *Brachycerae*. Possibly the resemblance between *E. elatum* and *E. elongatum* is due to independent parallel development from these two groups.

HYBRIDS †.

In the first half of the nineteenth century there appeared in European gardens several *Epimediums* unlike any occurring wild, which are usually referred as varieties to *E. grandiflorum*, *E. alpinum* or *E. pinnatum*. They were illustrated at the time, and most of them can be confidently identified with plants still cultivated. These blend the characters of species which have long been grown in gardens but do not occur together (with the possible exception of *E. grandiflorum* and *E. diphylum*) in nature. The supposition that they are garden hybrids alone accords with their morphology and what is known of their history.

† If, as observation suggests, each clone of *Epimedium* is self-sterile, i.e. able to form seed only when pollinated by another clone, the occurrence of hybrids and the rarity of seed-production under cultivation may be conjointly explained; of certain kinds the whole cultivated stock probably belongs to one clone, propagated by rhizome division, and in most gardens there is little likelihood of any *Epimedium* being represented by more than one clone; if any cross-pollination takes place, it must be between clones of different species, and differences in flower-colour, flowering time, etc., and lack of propinquity render this infrequent, but any seed thus produced will yield hybrids.

Their probable parentage is indicated below, the dates being approximately those when they were first introduced or noticed :—

E. grandiflorum (1830) \times *E. alpinum* (1580) = \times *E. rubrum* (1854) †.

E. grandiflorum (1830) \times *E. pinnatum* ? β *colchicum* (1840) = *E. versicolor* α , γ (1849), β (1854), δ (1932).

E. grandiflorum (1830) \times *E. diphylum* (1830, but long cultivated with *E. grandiflorum* in Japan) = \times *E. Youngianum* α (1839), β (1849), γ (1866).

E. Perralderianum (1867) \times *E. pinnatum* β *colchicum* (1840) = \times *E. Perralchicum* (1932).

E. pinnatum β *colchicum* (1840) \times *E. alpinum* (1580) = \times *E. warleyense* (1909).

Plants apparently derived from *E. pinnatum* have an occasionally leafless flower-stalk, broadly ovate sepals, and long stamen-filaments; those from *E. grandiflorum* rather long spurs, developed at base into distinct petaloid laminae tending to enclose the stamens; those from *E. diphylum* obovate petals with spurs of varying length or even absent; those from *E. alpinum* dark red sepals, etc. \times *E. Youngianum* may be a natural hybrid. According to Spae, his \times *E. lilacinum*, a plant near, if not identical with, *E. concinnum* Vatke, resulted from the deliberate crossing of *E. (Aceranthus) diphylum* and *E. violaceum* (*E. grandiflorum* γ *violaceum*). Since they have been much misunderstood and for the most part have not been adequately described, accounts of these hybrids are given below :—

i. \times *E. PERRAL-CHICUM* Stearn (*E. Perralderianum* \times *E. pinnatum* β *colchicum*).

Grex hortensis sect. *Rhizophylli*, calcaribus petalorum leviter curvatis, quoad formiam texturam magnitudinem foliolorum nunc ad *E. Perralderianum* nunc ad *E. pinnatum* β *colchicum* vergens. Specimina authentica in herbario Universitatis Cantabrigiensis ! Kew ! Stearn !

In the Royal Horticultural Society's garden at Wisley, Surrey, there grow together various forms of *Epimedium* section *Rhizophyllum* derived from a planting made some time between 1878 and 1902 by the former owner, George Ferguson Wilson (1822–1902); most of them agree exactly with neither *E. Perralderianum* nor *E. pinnatum* β *colchicum*, but combine in various ways their features.

Thus in one form (Wisley Hybrid, no. 1) the leaves have usually three leaflets, occasionally five, and these are somewhat larger (up to 11 cm. long, 8 cm. broad) than those of typical *E. Perralderianum* (up to 9 cm. long, 7 cm. broad under the same conditions), but more undulate and spiny at the margin than those of *E. pinnatum* β *colchicum* (which here go up to 14 cm. long, 9·5 cm. broad).

In another form (Wisley Hybrid, no. 2) the leaves have usually five leaflets, occasionally three, of much firmer texture, more undulate margin, with longer and more numerous spines, and prevailingly smaller size (up to 10·5 cm. long, 7·5 cm. broad) than those of typical *E. pinnatum* β *colchicum*. Its trifoliolate

† Cf. Déodart Spae in *Belgique Hort.* viii, p. 279 (1858).

leaves resemble those of *E. Perralderianum*. Its five-foliolate leaves are unique, since, although the two lower petioles are of normal length (2.5 to 4.5 cm. long), the remarkable shortness of the three upper petiolules (the two laterals 1 to 8 mm. long, the middle one 1 to 2 cm. long, by contrast with the 2.5 to 4 cm. long lateral and 4.5 to 5 cm. long middle petiolules of *E. pinnatum* β *colchicum*) causes their leaflets frequently to overlap conspicuously. Such a leaf may be described as like that of *E. Perralderianum*, with, however, the terminal leaflet replaced by three short-stalked or almost sessile leaflets, thus representing a compromise between the constantly trifoliolate leaf of that species and the frequently five-foliolate leaf of *E. pinnatum* β *colchicum*.

A third form, usually trifoliolate, diverges from these in the two basal lobes of the leaflet overlapping behind the insertion of the petiolule, sometimes for as much as 3 cm., so that the leaflet (up to 12 cm. long, 8 cm. broad, of firm texture and with long marginal spines) is more or less peltate.

The marginal spines range in length from about 0.5 to 1.9 mm. in *E. Perralderianum*, 0.2 to 1.3 mm. in the first-mentioned form (Wisley Hybrid, no. 1), 0.8 to 2.6 mm. in the second (Wisley Hybrid no. 2) 0.05 to 0.9 mm. in *E. pinnatum* β *colchicum*. The approximately 2 mm. long brown spur of the petal, though stouter and more upcurved in both forms than the straight spur of *E. pinnatum* β *colchicum*, is not bent so erect as that of *E. Perralderianum*.

E. Perralderianum and *E. pinnatum* β *colchicum* differ principally in the prevailing number, texture, and spininess of their leaflets and the form of the petal-spur. The above forms—and there are others which resemble *E. pinnatum* β *colchicum* more closely—thus bridge the slight morphological gap between these species. They are unknown in a wild state. Since *E. Perralderianum* and *E. pinnatum* β *colchicum* grow with them at Wisley one can only conclude that the crossing of these species and the back-crossing of their descendants during the last thirty or more years has bred the present assemblage of intermediate forms for which the abbreviated formula \times *Epimedium Perral-chicum* is accordingly proposed.

ii. \times E. RUBRUM C. Morren (*E. alpinum* \times *E. grandiflorum*).

E. rubrum C. Morr. in Belgique Hort. iv, p. 33, t. 6, figs. 1–6* (1854) : Regel, Gartenflora, vi, p. 21 (1857) ; xi p. 311, t. 373* (1862), & V'stnik Rossiiskago Obshestva [Journ. Russ. Hort. Soc.], 1862, p. 391, t. 99* (1862) : Baker in Gard. Chron. N.S. xiii, p. 620 (1880) : Ito in Journ. Linn. Soc., Bot. xxii, p. 431 p.p. (1887). *E. purpureum* Vilmorin-Andrieux, Fleurs Pleine Terre, ed. 2, p. 299 (1866) : Grönland & Rümpler, Vilmorin's Ill. Blumeng. i, p. 472 (1873). *E. alpinum* var. *rubrum* (C. Morr.) Hook. f. in Bot. Mag. xciii, t. 5671* (1867) : E. Morr. in Belgique Hort. xviii, p. 199, t. 14, fig. 2* (1868) : Franch. in Bull. Soc. Bot. France, xxxiii, p. 107 (1886) : L. H. Bailey, Cycl. Am. Hort. ii, p. 536 (1900), & Stand. Cycl. Hort. ii, p. 1122 (1914) : Wehrhahn, Gartenstauden, i, p. 454 (1930). *E. nigrum* hort. ex The Garden, xxi, p. 284, nomen nudum (1882). *E. alpinum* f. *rubrum* (C. Morr.) Voss, Vilmorin's Blumeng.

1, p. 50 (1894). *E. coccineum* Silva Tarouca, Unsere Freiland-Stauden, p. 93 (1910); ed. 2, p. 167 (1913), & ed. 3, p. 191 (1922): Heydenrich in Gartenflora, LXXXVI, p. 52 cum icone (1937). ? *E. Youngianum* f. *rubrum* A. Lehmann, Gartenzierpflanzen, ed. 2, p. 111 (1937).

Figures.—Belg. Hort. IV, t. 6* & XVIII, t. 14*; Gartenflora, XI, t. 373*; Bot. Mag. t. 5671*; V'stnik Ross. Obshest. 1862, t. 99*; Wehrhahn, Gartenst. p. 453; Gartenflora, LXXXVI, p. 53, as *E. coccineum* (1937).

Plant in flower 25–35 cm. high. Rhizome elongated, \pm 3 mm. thick. Leaves basal and caudate, usually biternate, sometimes triternate or with the secondary petiolules 5-foliolate; leaflets ovate or narrowly ovate, the tip acuminate, sometimes 2- or 3-fid, the margin spinous serrate, the base deeply or shallowly cordate, at first pubescent beneath, later subglabrous, membranous in texture, often bright red when young, up to 14 cm. long, 9 cm. broad. Flowering stem bearing one (abnormally two) bi- or triternate leaf; inflorescence compound, loose, glabrous or sparsely pilose, many-(10–23)-flowered, shorter, equalling or overtopping the stem-leaf; lower peduncles often 5-flowered; pedicels 1–2 cm. long. Flowers 1.5–2.5 cm. across. Outer sepals ovate-oblong, grey, speckled red, 3–4 mm. long, 1.5–3 mm. broad. Inner sepals narrowly oblong-ovate, blunt, concave, light crimson-carmine or cochineal-carmine, 1–1.2 cm. long, 4–5 mm. broad. Petals about as long as or shorter than the inner sepals, slipper-like, cylindric, pale yellow or white, tinged with red, 1 cm. long, with inflated blunt tips curving upwards and slight or distinct rounded basal laminae, to 4 mm. high, tending to enclose the stamens. Stamens included or slightly protruding, 4 mm. long; anthers 3 mm. long.

This striking plant is unknown in a wild state (though stated by Hooker to have been 'originally introduced into the St. Petersburg gardens from Japan in 1844') and is by many authors considered merely a large-flowered variety of *E. alpinum*, from which it differs not only in its larger and brighter flowers but also in its less rampant rhizome, and its more tapering, slightly upcurved petal-spurs, which are expanded at base into laminae tending to enclose the stamens as in *E. grandiflorum*. It was first noted, sometime before 1854, in Belgium, probably at the Ghent Botanic Garden, and there considered by some a species introduced from Japan, by others a hybrid raised by Donckelaar; the St. Petersburg garden obtained it, not from Japan, but from England, and there seems no doubt of its being a garden hybrid of European origin. I have received plants as *E. alpinum* var. *rubrum*, *E. purpureum*, *E. coccineum* (from an Austrian garden), *E. nigrum*, and 'E. pubigerum'. It is more ornamental than *E. alpinum*.

iii. \times *E. VERSICOLOR* C. Morren, sensu lato (*E. grandiflorum* \times *E. pinatum*? β *colchicum*).

The above name is here used collectively for a group of plants, unknown outside gardens, which seem to be hybrids between *E. grandiflorum* and

E. pinnatum (probably β *colchicum*). They have the following features in common :—

Plant in flowers 20–50 cm. high. Rhizome 3–5 mm. thick. Leaves basal and caudine, usually biternate, sometimes triternate or 5- or 3-foliate; leaflets ovate or narrowly ovate, acute or acuminate, the margin spinous-serrate, sparingly pubescent beneath, usually perishing in autumn in α *versicolor* (as in *E. grandiflorum*), but some remaining green all winter in γ *sulphureum* and δ *neo-sulphureum* (as in *E. pinnatum* β *colchicum*). Flowering stem leafless (as in *E. pinnatum*) or bearing one biternate, or rarely 3-foliate, leaf (as in *E. grandiflorum*) on the same plant; inflorescence usually simple, many (8–20) flowered, sometimes with 2–5-flowered lower peduncles. Flowers 2 cm. across, in general form like those of *E. grandiflorum* but smaller and possessing shorter petal-spurs and broader inner sepals (thus approaching *E. pinnatum*). Inner sepals broadly ovate, subacute or blunt, 10–14 mm. long, 5–8 mm. broad. Petals shorter or slightly longer than the inner sepals, yellow, with distinct petaloid basal laminæ 5–6 mm. high and cylindric spurs slightly upcurved and globular at their tips. Stamens usually included, 4·5 mm. long; anthers yellow, 3 mm. long.

Morren noted the ‘énorme raccourcissement des éperons [petals], leur terminaison en globules et le développement proportionnellement considérable dans la largeur des pétales’ [inner sepals] as features distinguishing these plants from *E. grandiflorum* (*E. macranthum*), but overlooked the occasionally leafless flowering stem, which also connects them with *E. pinnatum*. The following are quite distinct for garden purposes and, being propagated by division, are here designated as clones :—

Clon α VERSICOLOR (C. Morr.) Stearn.

E. macranthum var. *versicolor* C. Morr., Ann. Soc. Agric. Bot. Gand, v, p. 91 (1849); Wehrhahn in Bonstedt, Pareys Blumeng. I, p. 621 (1931). *E. versicolor* C. Morr., op. cit. p. 92, t. 243, fig. 2* (1849); Franch. in Bull. Soc. Bot. France, XXXIII, p. 115 (1886); Komarov in Acta Hort. Petrop. XXIX, p. 133 (1908); Wehrhahn, Gartenstauden, I, p. 454 (1930), sensu stricto. *E. discolor* Vilmorin-Andrieux, Fleurs Pleine Terre, ed. 2, p. 297 (1866); Grönland & Rümpler, Vilmorin's Ill. Blumeng. I, p. 472 (1873). *E. macranthum* f. *versicolor* (C. Morr.) Voss, Vilmorin's Blumeng. I, p. 51 (1894).

Figure.—Ann. Soc. Agric. Bot. Gand, v, t. 243, fig. 2*.

Leaflets usually 9, conspicuously mottled or entirely red when young, later green, the basal lobes rounded, acute or acuminate and often diverging widely, membranous in texture and perishing in autumn, up to 10 cm. long, 6 cm. broad. Inflorescence glandular, with 10–20 flowers. Inner sepals old rose. Petals yellow, with red-tinged spurs.

This differs from *E. versicolor* γ *sulphureum* in the conspicuous red colouring of its young foliage, its more glandular inflorescence, its more acuminate leaflets of thinner texture, and its rose sepals. It is also of less vigorous growth

and rarer in gardens. The above account is from plants grown in the 'Wilder-
ness' of St. John's College, Cambridge.

Clon β CUPREUM C. Morren.

E. versicolor cupreum C. Morr. in Belgique Hort. iv, p. 34, t. 6, fig. 7* (1854) : Franch., loc. cit. (1886) ; Komarov, loc. cit. (1908) : Wehrhahn, loc. cit. (1930).

E. macranthum f. *versicolor cupreum* Voss, loc. cit. (1894).

Figure.—Belg. Hort. iv, t. 6, fig. 7*.

This is like *E. versicolor* α *versicolor*, but the inner sepals ('petales' Morr.) are coppery-red ; 'la couleur des pétales est aussi remarquable que rare dans la végétation, c'est le rouge saumoné clair ou le rouge cuivré' (Morr., loc. cit.).

Clon γ SULPHUREUM (C. Morr.) Stearn.

E. macranthum var. *sulphureum* C. Morr., Ann. Soc. Agric. Bot. Gand, v, p. 91 (1849) : Wehrhahn in Bonstedt, Pareys Blumeng. I, p. 621 (1931). *E. sulphureum* C. Morr., op. cit. p. 92, t. 243, fig. 3* (1849) : Vilmorin-Andrieux, Fleurs Pleine Terre, ed. 2, p. 297 (1866) : Franch. in Bull. Soc. Bot. France, xxxii, p. 115 (1886) : Komarov in Acta Hort. Petrop. xxix, p. 133 (1908) : Wehrhahn, Gartenstauden, I, p. 455 (1930). *E. citrinum* Baker (!) in Gard. Chron. N.S. xiii, p. 683 (1880) : Stearn in Gardening Illust. LIV, p. 31 (1932). *E. macranthum* f. *sulphureum* Voss, Vilmorin's Blumeng. I, p. 51 (1894). *E. ochroleucum* Farrer, English Rock Gard. I, p. 327 (1919). *E. pinnatum sulphureum* Bergmans, Vaste Pl. p. 203 (1924). *E. versicolor* var. *sulphureum* (C. Morr.) Stearn in Kew Handlist of Rock Gard. Pl. ed. 4, p. 53 (1934).

Figures.—Ann. Soc. Agric. Bot. Gand, v, t. 243, fig. 3* ; Gartenflora, LXXXVI, p. 53, as '*E. pinnatum*' (1937).

Leaflets 5–11 (usually 9), green or sometimes red or brown mottled, the base deeply cordate, with usually rounded lobes, subcoriaceous in texture and sometimes remaining green all winter, up to 8 cm. long, 6 cm. broad. *Inflorescence* usually glabrous, with 8–20 flowers ; pedicels 5–25 mm. long. *Inner sepals* pale yellow ('Martius yellow', Ridgeway, Col. Stand. t. iv, 23 f.). *Petals* usually about as long as the inner sepals and brighter yellow ('pale lemon yellow', Ridgeway, t. iv, 23 b.).

This is a graceful plant with pendulous lemon-yellow flowers, common in gardens and usually called *E. sulphureum*, '*E. pinnatum*' or *E. ochroleucum*. From *E. pinnatum*, with which it is confused, it differs in its paler flowers with longer spurred laminate petals and usually included stamens, as also its frequently leafy flowering stem. Baker's *E. citrinum* (sp. authent. ex hort. Ware in K. !) is identical with Morren's *E. sulphureum*. As Baker says, 'it is most like a yellow-flowered variety of *macranthum* [= *grandiflorum*], but differs by its short spur and the racemes being simple and sometimes produced direct from the rootstock'.

Clon δ NEO-SULPHUREUM Stearn, var. nov. (Pl. 31.)

Folia plerumque 3-, interdum 5- vel 9-foliolata; *foliola* ovata vel anguste ovata. *Caulis florifer* aphyllus vel monophyllus; *inflorescentia* simplex, subglabra, 7-16-flora; *pedicelli* 1-3 cm. longi. *Flores* c. 2 cm. diam., flavi, eis *E. versicolor* γ sulphurei subsimiles sed calcaribus petalorum brevioribus. Specimina authentica in herbario Universitatis Cantabrigiensis! Mus. Brit.! Kew! Stearn!

Plant in flower 20-50 cm. high. *Basal leaves* usually 3-, less often 5- or 9-foliolate: *stem-leaves* nearly always 3-foliolate, occasionally 5- or 9-foliolate; *leaflets* ovate or narrowly ovate, acute or acuminate at the tip, the base cordate, with a rather open sinus sparsely pubescent beneath, up to 9 cm. long, 7 cm. broad. *Flowering stem* sometimes leafless, more often bearing one 3- or occasionally 5-foliolate leaf; *inflorescence* simple, loose, subglabrous, 7-16-flowered, overtopping the stem-leaf; *pedicels* 0.5-3 cm. long. *Flowers* 2 cm. across, pale yellow. *Outer sepals* purplish, 3-4 mm. long. *Inner sepals* narrowly ovate, bluish, flat, pale creamy yellow ('sulphur yellow', Ridgeway, v. 25 f.), 1-1.3 cm. long, 5-7 mm. broad. *Petals* shorter by 3-5 mm. than the inner sepals, with pale lemon-yellow laminae 5-6 mm. high, 6 mm. broad, enclosing the stamens, and brownish-tinged slightly upcurved spurs 3-4 mm. long. *Stamens* included, 4 mm. long; *anthers* 3 mm. long, yellow.

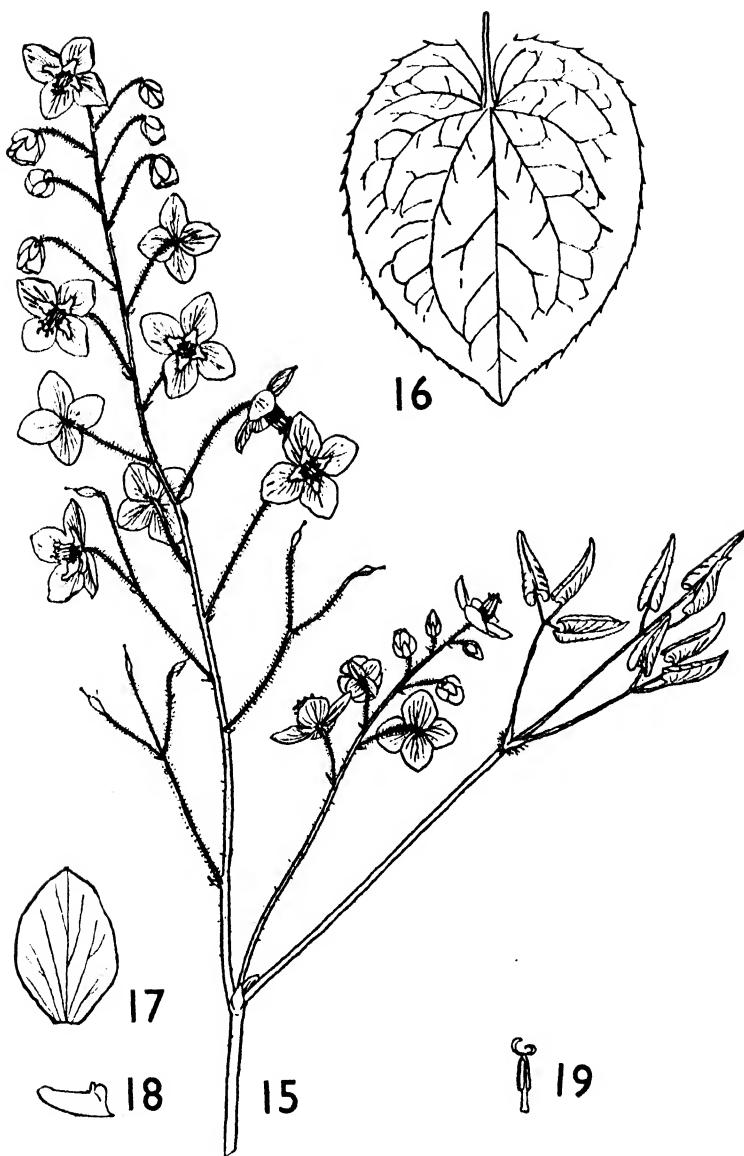
This attractive plant is very like $\times E. versicolor$ γ sulphureum, but its leaves, especially those on the flowering stems, consist usually of 3 leaflets (in sulphureum nearly always of 9 leaflets), and the spurs of the petals are always distinctly shorter than the inner sepals. Beginning to flower in April, it finishes in mid or late May, a fortnight or more after *E. sulphureum*. It has long been cultivated in the Royal Horticultural Society's Garden at Wisley, Surrey, and distributed thence to other gardens, but it is by no means so common as *E. sulphureum*. The young leaves are brownish.

iv. $\times E. WARLEYENSE$ Stearn (*E. alpinum* × *E. pinnatum* β colchicum).

Figure.—Stoker, A Gardener's Progress, t. 11 facing p. 163 (1938).

Origo hujus stirpis amoena obscura est, sed per multos annos hortum Warleyensem cel. dominae Willmottiae ornavit; cum formis feris non quadrat, ac ob proprietatem inter *E. alpinum* et *E. pinnatum* β colchicum medians hybrida hortensis videtur. Ab $\times E. versicolori$ petalorum forma et magnitudine et antheris exsertis, ab *E. alpino* et *E. pinnato* caule florifero aut aphylo aut foliato, sepalis interioribus rubro-cupreis praecipue distinguitur. Specimina authenticata in herbario Universitatis Cantabrigiensis! Kew! Stearn!

Plant in flower 20-55 cm. high. *Rhizome* elongated, 4-8 mm. thick. *Leaves* basal and caudine, 9- or 5- (rarely 3-) foliolate; *leaflets* ovate or broadly ovate, the tip acute, the margin sparsely spinous-serrate, the base deeply cordate, with rounded or acute lobes, finely pubescent beneath, green when young, becoming subcoriaceous with age and often remaining green all winter, up to 13 cm. long, 9.5 cm. broad. *Flowering stem* leafless or with one 5- or 9-foliolate



FIGS. 15-19.—*E. warleyense*. 15, the inflorescence, $\times 1$; 16, a leaflet, $\times 1$; 17, an inner sepal, $\times 3$; 18, a petal, $\times 2$; 19, a stamen, $\times 2$.

leaf; *inflorescence* simple or compound, glandular, 10–30-flowered, with sometimes a large secondary raceme in the leaf-axil; lower peduncles often 5-flowered; *pedicels* 1–2 cm. long. *Flowers* 1·5 cm. across. *Outer sepals* green or purple-tinged, obovate, blunt, 3–4 mm. long. *Inner sepals* ovate-oblong, blunt, ‘coppery red’ or ‘orange pink’ in effect, the yellow ground-colour being conspicuously tinged and veined with red (‘rouge cerise’), especially in the opening flower, fading to a yellowish salmon colour, 8 mm. long, 5 mm. broad. *Petals* much shorter than the inner sepals, yellow (‘jaune safran’), with blunt, occasionally red-streaked spurs scarcely 4 mm. long and small bilobed (not erose) laminae about 3 mm. across, 3 mm. deep. *Stamens* protruding, 4·5 mm. long; *anthers* 2·5 mm. long, greenish. It flowers from early April into May.

This decorative plant is of unknown origin. I received it as ‘*E. Perralderianum*’ (non Cosson) in 1932 from the late Miss Ellen Ann Willmott (1858–1934) in whose garden at Great Warley †, Essex, it had flourished for over twenty years. Before the Great War Miss Willmott intended to prepare a work on *Epimedium* similar to her ‘Genus Rosa’, and this plant (‘a glorified *E. alpinum*’) was among the many Epimedums she acquired in preparation for it. *E. warleyense* cannot be referred, even as a variety, to any known species; its characters suggest that it is a garden hybrid between *E. alpinum* and *E. pinnatum* β *colchicum*. At one time I called this *E. Willmottiae*, a name inadvertently mentioned, but not validly published, by E. S. Lyttel in My Garden, XII, p. 486 (Dec. 1937). Fig. 15 over-emphasizes the hairiness of the pedicels.

v. \times *E. Youngianum* Fischer & Meyer, sensu lato (*E. diphylum* \times *E. grandiflorum*).

The name *E. Youngianum* is here used collectively to cover all plants of the supposed parentage *E. (Aceranthus) diphylum* \times *E. grandiflorum*, this being the earliest binomial applied to a member of the group which comprises Wehrhahn’s ‘Hybridengattung’ *Bonstedtia* :—

Plant in flower 10–30 cm. high. *Leaves* basal and caudine, 2–9-foliolate; *leaflets* ovate to narrowly ovate, thin in texture, and becoming subglabrous beneath. *Flowering stem* bearing one 2–9-foliolate leaf; *inflorescence* simple or with the lower peduncles 2-flowered, almost glabrous, few-(3–12)-flowered; *pedicels* 5–20 (rarely up to 40) mm. long. *Flowers* campanulate, pendulous, white or rose, 1·6–2 cm. across. *Inner sepals* narrowly ovate to lanceolate, blunt or subacute, horizontally spreading, 8–11 mm. long, 3–5 mm. broad. *Petals* broader and slightly shorter than the inner sepals, obovate, rounded, connivent, 7–10 mm. long, 4–6 mm. broad, spurless or with a short conical dorsal projection or a slender incurving subulate spur sometimes (in α *typicum*)

† The name ‘Warley’ is apparently of old English origin, but obscure in meaning, eleventh-century forms, according to P. H. Reaney (Place-names of Essex, p. 133; 1935), being ‘Warelia’ (1086), ‘Wareleia’ (1086), and ‘Werle’ (c. 1045).

up to 1 cm. long, frequently varying in length and form on the same inflorescence. *Stamens* included, 3-4 mm. long; *anthers* 2.5-3 mm. long.

The following clones differ in habit, leaf, and flower-colour. In α *typicum* the leaf has nine leaflets: β *roseum* and γ *niveum* tend to suppress the middle three; their leaves usually consist of six leaflets (fig. 20, C), although leaves varying from the binate form (A) typical of *E. grandiflorum* through intermediates (B, C, D) known only in β *roseum* and γ *niveum* to the bifoliolate form (F) typical of *E. diphylum* may sometimes be found on one plant.

Clon α *TYPLICUM* Makino. (Pl. 31, fig. 2.)

'*E. Musschianum* Morr. & Dene', secundum Graham (!) in Edinb. New Phil. Journ. xxvii, p. 190 (1839); & in Bot. Mag. LXVI, t. 3745* (1839): Maund, Bot. Gard. XII, no. 1122, t. 281* (1848): Duncan in Gard. Chron.

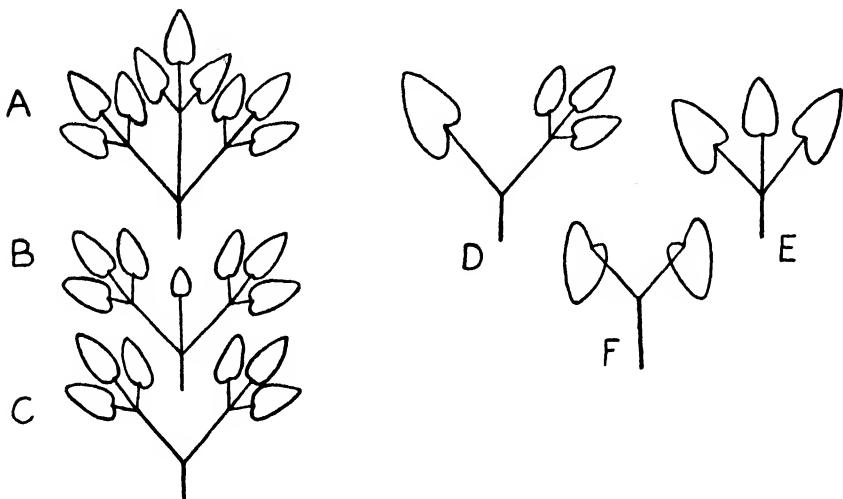


FIG. 20.—Diagrams of the foliage of \times *E. Youngianum*, vars. *roseum* and *niveum*.

1870, p. 698; vix Morr. & Dene. *E. Youngianum* Fisch. & Mey., Sert. Petrop. sub t. I (1846): Franch. in Bull. Soc. Bot. France, XXXIII, p. 115 (1886): Voss, Vilmorin's Blumeng. I, p. 51 (1894), & II, t. 5, fig. 2* (1895): Komarov in Acta Hort. Petrop. XXIX, p. 133 (1908), sensu stricto. 'Epimedium des Münchner Herbars als *Aceranthus sagittatus* oder *Ac. Ikarisoio* bezeichnet' Tischler (!) in Engl. Bot. Jahrb. XXXI, p. 665 (1902). *E. Youngianum* var. *typicum* Makino in Bot. Mag. Tokyo, XXIII, p. 142 (1909); Makino & Nemoto, Fl. Japan, ed. 2, p. 348 (1931). *E. Youngii* hort. ex Bergmans, Vaste Pl. p. 203, pro syn. (1924). *Bonstedtia Youngianum* (Fisch.) Wehrhahn, Gartenstauden, I, p. 455 (1930): Wehrhahn in Bonstedt, Parey's Blumeng. I, p. 621 (1931). *Bonstedtia lilacina* var. *Youngiana* (Fisch.) Kesselring in Silva Tarouca & Schneider, Unsere Freiland-Stauden, ed. 5, p. 99 (1934). ?*E. Musschianum* var. *vulgare* G. Koidzumi in Acta Phytotaxon., Kyoto, V, p. 127 (1936).

Figures.—Bot. Mag. t. 3745* (type of *E. Youngianum*) ; Maund, Bot. Gard. XII, no. 1122 * ; Voss, Vilmorin's Blumeng. t. 5, fig. 2 *.

Plant in flower 15–30 cm. high. *Leaves* usually biennial, but sometimes 3-foliolate (as figured in Bot. Mag. t. 3745) ; *leaflets* narrowly ovate or sometimes ovate, the tip abruptly long-acuminate, the margin sparsely or distinctly spinous-serrate, the base deeply cordate, with usually rounded lobes, ± 2–8 cm. long, 1–5 cm. broad. *Flowering stem* bearing one biennial leaf ; *inflorescence* with 3–8 flowers crowded towards its apex, much shorter than the stem-leaf ; *pedicels* 5–10 mm. long. *Flowers* (i.e. inner sepals and petals) white with a greenish tinge.

This plant, which may be a natural hybrid between *E. diphylleum* and *E. grandiflorum*, was introduced into European gardens from Japan by von Siebold, who called it 'erectum' ; it was known to Fischer and Meyer only from Graham's plate (Bot. Mag. t. 3745 ; sp. authent. in K. !), their new name (cf. p. 427) of *E. Youngianum* commemorating the Epsom nurserymen, Messrs. Charles, James and Peter Young, who supplied the plant to the Edinburgh Botanic Garden ; this Epsom nursery was celebrated for uncommon herbaceous plants (cf. Loudon's Gard. Mag. v, pp. 597–8 ; 1829), and published in 1828 an 'Hortus Epsomensis' enumerating 4060 kinds then in cultivation there. An interesting but horticulturally unattractive plant, hiding its few small flowers under its foliage, *E. Youngianum* α *typicum* is now rare in European gardens. It flowers in April, earlier than γ *nivale*, and is more often damaged by frost.

Clon β ROSEUM (Vilmorin-Andrieux) Stearn. (Pl. 31, fig. 3.)

? *E. violaceo-diphyllum* C. Morr. in Ann. Soc. Agric. Bot. Gand, v, p. 92 (1849). ? *E. hybridum* C. Morr., loc. cit. t. 243, fig. 1* (1849). ? *E. lilacinum* Donckelaar ex Morr., loc. cit. (1849) : Vilmorin-Andrieux, Fleurs Pleine Terre, ed. 2, p. 298 (1866) : Grönland & Rümpler, Vilmorin's Illust. Blumeng. I, p. 471 (1873) : Franch. in Bull. Soc. Bot. France, XXXIII, p. 113 (1886) : Komarov in Acta Hort. Petrop. XXIX, p. 132 (1908). *E. sinense*, *E. roseum*, *E. ultraroseum* Vilmorin-Andrieux (!), op. cit. p. 298 (1866) : Grönland & Rümpler, loc. cit. (1873). *E. concinnum* Vatke (!) in Regel, Gartenflora, XXI, p. 165, t. 726 (1872) : Baker in Gard. Chron. N.S. XIII, p. 683 (1880) : T. Ito in Journ. Linn. Soc., Bot. XXII, p. 431 (1887). 'E. sinense' hort. Berol. ex Vatke, loc. cit. pro syn. (1872). *E. Musschianum* *violaceum* hort. ex Baker, loc. cit. pro syn. (1880). *E. macranthum* f. *roseum* [Vilm.-Andr.] Voss, Vilmorin's Blumeng. I, p. 51 (1894). *E. macranthum* var. *roseum* (Voss) W. Miller in L. H. Bailey, Cycl. Am. Hort. II, p. 535 (1900). ? *E. japonicum* Makino in Iinuma, Somoku Dzus. ed. 3, II, p. 129 (71) in obs. Jap. (1907)†. *E. Youngianum* var. *concinnum* (Vatke) Makino in Bot. Mag. Tokyo, XXIII, p. 142 (1909) : Makino & Nemoto, Fl. Japan, ed. 2, p. 348 (1931). ? *E. Youngianum* var. *aceranthoides* Makino, loc. cit. (1909). ? *E. grandiflorum* var. *lilacissima* G. Anley, Alpine House Cult. p. 170, nomen subnudum (1938). *Bonstedtia lilacinum* (Donck.) Wehrhahn,

† See p. 525.

Gartenstauden, I, p. 455 (1930) ; Silva Tarouca & Schneider, Unsere Freiland-Stauden, ed. 5, p. 99 (1934). *E. Youngianum* var. *roseum* (Vilm.) Stearn in Kew Hand-list of Rock Gard. Pl. ed. 4, p. 54 (1934).

Figures.—? Ann. Soc. Agric. Bot. Gand, v, t. 243, fig. 1* (not characteristic) ; Gartenflora, XXI, t. 726 (poor) ; Journ. Jap. Bot. XIII, p. 811 (good).

Plant in flower 10–30 cm. high. Leaves very variable, 2-, 6- or 7-foliolate, rarely biennial; leaflets ovate, the lateral leaflets usually with very unequal basal lobes, the middle leaflet sometimes peltate and scoop-like, the tip blunt (not abruptly long-acuminate), the margin sparsely spinous-serrate, 2–5 cm. long, 1–2.5 cm. broad. Flowering stem usually bearing one 2- or 6-foliolate leaf; inflorescence loose, 4–12-flowered, about as long as or longer than the stem-leaf; pedicels 5–15 (rarely 40) mm. long. Flowers (i.e. inner sepals and petals) purplish-mauve, varying in depth of colour.

This plant is known in gardens under a variety of names, the commonest being *E. lilacinum* (cf., however, p. 525). Specimens dating from 1863 of the Epimediums briefly described in 'Les Fleurs de Pleine Terre' as *E. sinense* ('fleurs blanches très légèrement carnées'), *E. roseum* ('fleurs d'un rose clair') and *E. atroroseum* ('fleurs d'un rose foncée') are preserved in the Vilmorin-Andrieux herbarium at Verrières-le-Buisson near Paris, and agree with authentic specimens of *E. concinnum* Vatke (B. ! Weimar ! hb. Stearn ! Cantab. !), which was grown in the Berlin Botanic Garden as *E. sinense*. Vatke's description and figure of his *E. concinnum* are so unsatisfactory that Maximowicz and Franchet thought it synonymous with *E. rubrum* ! Baker (K. !), however, interpreted it correctly.

Clon γ NIVEUM (Vilmorin-Andrieux) Stearn. (Pl. 31, fig. 4.)

E. niveum Vilmorin-Andrieux (!), Fleurs Pleine Terre, ed. 2, p. 298 (1866) : Grönland & Rümpler, Vilmorin's Illustr. Blumeng. p. 471 (1873) : Baker in Gard. Chron. N.S. XIII, p. 683 pro syn. '*E. Musschianum*' (1880) : Koenemann in Gartenwelt, III, p. 591 cum icone (1889) : Farrer, English Rock Gard. I, p. 327 (1919). '*E. Musschianum* Morr. & Dene', Baker (!), loc. cit. p.p. quoad descript. et syn. hort. (1880) : T. Ito in Journ. Linn. Soc., Bot. XXII, p. 431 p.p. (1887) : Silva Tarouca & Schneider, Unsere Freiland-Stauden, ed. 5, p. 161, fig. 162 (1934) : Heydenreich in Gartenflora, LXXXVI, p. 54 cum icone (1937) : vix Morr. & Dene. *E. macranthum* f. *niveum* [Vilmorin-Andrieux] Voss, Vilmorin's Blumeng. I, p. 51 (1894). *E. macranthum* var. *niveum* (Voss) W. Miller in L. H. Bailey, Cycl. Am. Hort. II, p. 535 (1900). '*Bonstedia lilacinum*' Wehrhahn, Gartenstauden, I, p. 455, p.p. (1930). '*E. macranthum* var. *Musschianum*' Wehrhahn, loc. cit. p.p. (1930) ; specimina a cel. Lemperg. mihi communicata et a cel. Wehrhahn. determinata ! *E. Youngianum* var. *niveum* Stearn in Kew Hand-list of Rock Gard. Pl. ed. 4, p. 53 (1934).

Figures.—Gartenwelt, III, p. 591 : Silva Tarouca & Schneider, Unsere Freiland-Stauden, ed. 5, p. 159, fig. 162 (good) ; Gartenflora, LXXXVI, p. 53, as '*E. Musschianum*' (1937).

This is a low, neat plant, in habit like *E. roseum*, but possessing pure white flowers. It differs in its blunt leaflets (which vary in number from 2 to 9) and looser inflorescence (with pedicels 5–20 mm. long) usually overtopping the stem-leaf from *E. typicum*, with which Baker confused it. When all its flowers are spurless and its leaves 2-foliate, as occasionally happens, it cannot be distinguished from *E. diphyllum*, but usually spurred and spurless flowers and leaves with 2, 3, 6 or even 9 leaflets may be found on one plant. It has considerable garden-merit, being small, dainty and easier to grow than *E. diphyllum*, and flowers from May into early June, later than *E. typicum*. The name *E. niveum* appeared in the Belgian nurseryman Van Houtte's catalogue before 1860.

OBSCURE AND EXCLUDED SPECIES.

Epimedium angustifolium W. T. Macoun, List. Per. Expt. Farm, Gard. Ottawa (Bull. Cent. Exp. Farm. Ottawa, ser. 2, no. 2, no. 5) p. 40 (1908). ‘Half-hardy, 8–12 in. Fl. white. May 11 to May 22’ (Macoun, loc. cit.). Perhaps *E. Youngianum* γ *niveum*.

Epimedium Cavaleriei H. Léveillé (!), Cat. Pl. Yunnan, p. 18 in adnot. (1915) = *Stauntonia Cavaleriana* Gagnepain (1908), described from the same gathering. A shrub belonging to the Lardizabalaceae.

Epimedium japonicum Makino in Iinuma, Somoku Dzus. ed. 3. II, p. 129 in obs. Jap. sub t. 46 (1907), non Siebold ex Miq.

This is known to me only from Makino's brief note, published in Japanese and here translated:—‘Herbaceous. One stem with three leaflets. Flowers as in the former [*E. diphyllum*], but pale pink. This should be another species of the genus and be called *Epimedium japonicum* Makino. The petals are spurred, but in the baikwa-ikariso [*E. diphyllum*] they are flat. Is it a form intermediate between the baikwa-ikariso [*E. diphyllum*] and the ikariso [*E. grandiflorum*]?’ The name *E. japonicum* does not occur in Makino & Nemoto's Flora of Japan, ed. 2 (1931); it may be a synonym of \times *E. Youngianum* β *roseum*.

Epimedium lilacinum Donckelaar ex C. Morr. Ann. Soc. Agric. Bot. Gand, v, p. 91 (1849). *E. hybridum* C. Morr., op. cit. p. 91, t. 243, fig. 1* (1849). *E. violaceo-diphyllum* C. Morr., loc. cit. (1849).

The plant cultivated today as *E. lilacinum* (for which the name \times *E. Youngianum* β *roseum* is here adopted) seems distinct from the original *E. lilacinum* (*E. diphyllum* \times *E. violaceum*, fide D. Spaë ex Morr., loc. cit.) as figured by Morren, the spurs of the latter being apparently stouter and the leaflets different. Morren describes *E. lilacinum* as having ‘les feuilles des vrais épimèdes, la forme cordée, les lobes arrondis, les dents nombreuses et la seule ressemblance que j'y vois avec les feuilles de l'aceranthus [*Aceranthus diphyllus* = *E. diphyllum*] se borne à leur existence géminée . . . Il n'y a rien dans ces fleurs qui rappelle l'*Aceranthus*: elles sont armées de vrais nectaires [petals] cuculliformes et

l'éperon même est en pointe ; les pétales [inner sepals] sont planes, grands, dépassent un peu les nectaires [petals] en longeur et le coloris est celui de l'*Epimedium violaceum* [=*E. grandiflorum* γ *violaceum*], lilacine, lavée de blanc et de violet'. I have no doubt that this plant and our \times *E. Youngianum* β *roseum* (*E. concinnum* Vatke) are hybrids of the same parentage, but they probably represent distinct clones. Unfortunately no plant corresponding exactly to Morren's plate seems to be in cultivation today, the nearest being \times *E. Youngianum* β *roseum* ; it may be that the latter was incorrectly figured.

Epimedium Musschianum Morr. & Dene in Ann. Sci. Nat. Bot. ser. 2, II, p. 353 (1834) : Franch. in Bull. Soc. Bot. France, XXXIII, pp. 111, 114 (1886). *E. macranthum* var. *Musschianum* (Morr. & Dene) Makino in Bot. Mag. Tokyo, XXIII, p. 143, quoad syn. (1909). '*E. parvulum* Baker' ex Koidzumi in Acta Phototaxon., Kyoto, v, p. 126, pro syn. (1936).

Because of its uncertain application, the name *E. Musschianum* is best abandoned. It is unfortunate that Morren and Decaisne published no figure and left no type-specimen at Paris or Bruxelles since, as Franchet remarked, 'la longue description qu'ils en donnent ne dit absolument rien qui puisse mettre sur la trace de son identité'. They placed it between *E. macranthum* and *E. violaceum*, distinguishing it from other species 'par ses feuilles simplement ternées, d'une couleur verte forcée, par ses fleurs d'un blanc sale, moins grandes que dans l'espèce précédente'. No species with such characters is known today, although it is possible Morren and Decaisne had before them an abnormal plant of *E. grandiflorum* β *normale* or a state of the hybrid between *E. diphyllum* and *E. grandiflorum*. There is a specimen (!) in the Paris Museum labelled '*E. Musschianum*' which Franchet regarded as authentic—'l'étiquette est de la main de Decaisne'. This specimen belongs to *E. sagittatum* (*E. sinense*) ; the handwriting on the label (ex herb. Lugd. Bat., i.e. Leiden) is not, however, Decaisne's, but that of the Leiden botanist Blume ; the note of affirmation on this sheet is by Spach, and possibly Decaisne never saw it at all. The original description of *E. Musschianum* definitely excludes *E. sagittatum*.

The name commemorates Jean Henri Mussche (1764–1834), head gardener at the Ghent Botanic Garden and author of the 'Hortus Gandavensis' (1817) ; cf. N. Cornellissen, Quelques souvenirs . . . de Jean Henri Mussche (1835).

For '*E. Musschianum*', Bot. Mag. t. 3745, see \times *E. Youngianum* α *typicum* (p. 522).

Epimedium Musschianum var. *multifoliolatum* G. Koidzumi in Acta Phototaxon., Kyoto, v, p. 126 (1936).

'Folio caulinato quater ternato. Hab. Japonia occidentalis' (Koidz., loc. cit.). *E. pteroceras* C. Morr. in Ann. Soc. Agric. Bot. Gand, I, pp. 145–6, t. 14* (1845) ; II, p. 140 in obs. (1846) : Franch. in Bull. Soc. Bot. France, XXXIII, pp. 114–15 (1886).

Figure.—Ann. Soc. Agric. Bot. Gand, I, t. 14*.

From Morren's account and plate this should be a distinct plant, but nothing exactly corresponding with it has been seen since; there is no type at Paris, Liège or Bruxelles. Morren describes it as follows (non-essential details being here omitted) :—

' Caule subpedali foliis triternatis, foliolis bi-tripollicaribus, late cordatis, obtusiusculis, argute-dentatis spica terminali, apice nutante, multi-flora calyce tetraphyllo, foliolis ovato-oblongis, flavis; petalis infimis quatuor, ovatis, basi rotundatis, apice obtusis, superis nectariformibus, brevioribus, cucullatis, basi valde dilatatis, inflatis, bialatis, apice obtuso, semitereti, cavo, nectarifero, purpureo les fleurs sont en épi long et d'un jaune d'or, mais ce qui distingue surtout, ce sont les bases dilatées et ailées des nectaires ou seconde pétales d'après les renseignements qui nous ont été communiqués par M. Jacob-Makoy: elle viendrait du Caucase' (Morren, 1845).

Morren again refers to this plant in 1846 when figuring *E. pinnatum* (β *colchicum*), which, he says, 'porte un épi fort riche de fleurs jaunes. Celles-ci sont beaucoup plus grandes et plus nombreuses que celles de l'*Epimedium pteroceras* qui diffère d'ailleurs considérablement de cette espèce-ci par sa tige feuillée, par ses feuilles triternées, par les ailes de ses nectaires' (Morren, 1846). In Morren's plate there is no indication of a stem-leaf. According to this plate the leaf is 9-foliolate (as in *E. pinnatum* α *originarium*), the inflorescence simple and bearing about 20 starry yellow flowers about 1·5 cm. across, with narrow, elliptic, inner sepals and minute petals; the spur of the petal is brown-tipped and slightly upcurved (much as in *E. pinnatum* β *colchicum*) and probably 2–3 mm. long, but the slight basal lamina is entire; the filaments of the very exserted stamens are 1½ times as long as the brownish anthers.

Attention is drawn to this obscure plant in the hope that it may be rediscovered. It is apparently between *E. pinnatum* α *originarium* and β *colchicum*, but distinct from both in the non-lacerate laminae of the petals.

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The references in parenthesis are to Bretschneider's History (1898), e.g. B. II, p. 954, or to Fournier's Voyages (1932), e.g. F. II, p. 101, where information regarding collectors in China may be found; Handel-Mazzetti (1927 a) and Limpricht (1922) have themselves published detailed accounts, with maps, of their travels.

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Baikwa ikariso (Japan)	<i>Epimedium diphyllum</i> , cf. p. 488.
Barrenwort (England)	Originally <i>E. alpinum</i> ; now used as a general name for the whole genus; cf. p. 476.
Bischofsmütze (Germany)	<i>E. alpinum</i> ; also whole genus.
Bisschopsmuts (Holland)	Do,

Chi chu tso (China)	<i>E. grandiflorum.</i>
Chi liang ching (China)	<i>E. grandiflorum</i> , cf. p. 484.
Elfenblume (Germany, fide K. Heydenreich).	<i>E. Youngianum</i> γ <i>nivcum</i> .
Epimède (France)	Whole genus.
Epimedio (Italy)	<i>E. alpinum</i> ; also whole genus.
Fang chang tsao (China)	<i>E. grandiflorum</i> , cf. p. 484.
Golden fleece Epimedium (U.S.A.)	<i>E. pinnatum</i> β <i>colchicum</i> .
Hozaki no ikariso (Japan)	<i>E. sagittatum</i> , cf. p. 508.
Hsien ling pi (China)	<i>E. sagittatum.</i>
Hwang li chu (China)	<i>E. grandiflorum.</i>
Ikarigusa (Japan)	<i>E. grandiflorum.</i>
Ikariso (Japan)	<i>E. grandiflorum</i> ; also whole genus; cf. p. 483.
Inside-out flower (U.S.A.)	<i>Vancouveria</i> , esp. <i>V. planipetala</i> .
Kanabikiso (Japan)	<i>E. grandiflorum.</i>
Kang chi chien (China)	<i>E. grandiflorum.</i>
Kan tze (China)	<i>E. grandiflorum.</i>
Kumoriso (Japan)	<i>E. grandiflorum.</i>
Kvespin (Jugoslavia)	<i>E. alpinum.</i>
Lipica (Jugoslavia)	<i>E. alpinum.</i>
Long spur Epimedium (U.S.A.)	<i>E. grandiflorum.</i>
Mexican ivy (U.S.A.)	<i>V. planipetala</i> (but sometimes <i>Cobaea scandens</i> !).
Muiltjesbloem (Holland)	<i>E. alpinum.</i>
Nu ko hwa (China)	<i>E. leptorrhizum</i> , cf. p. 500.
Oh baika ikariso (Japan)	<i>E. setosum.</i>
Redwood ivy (U.S.A.)	<i>V. planipetala.</i>
Sam chi ku yop pul (Korea)	<i>E. grandiflorum.</i>
Shan tzi kiu yeh tsao (San chi chui tso) (China)	<i>E. grandiflorum.</i>
Shi ling bee (China)	<i>E. grandiflorum</i> , cf. p. 484.
Skornice (Czechoslovakia)	Whole genus, esp. <i>E. alpinum</i> .
Sockenblume (Germany)	<i>E. alpinum</i> ; also general name for genus.
Tentori bana (Japan)	<i>E. grandiflorum.</i>
Tokiwa ikariso (Japan)	<i>E. semperflorens.</i>
Twin-leaf Epimedium, suggested for <i>E. diphylum</i>	<i>E. grandiflorum.</i>
Uin yang kak (Korea)	<i>E. grandiflorum.</i>
Umugi & Umugina (Japan)	<i>E. grandiflorum.</i>
Vimček (Jugoslavia)	<i>E. alpinum.</i>
Yen chang tsao (China)	<i>E. sagittatum</i> in China proper, <i>E. grandiflorum</i> in Manchuria.
Yim yong kok (Malaya)	<i>E. sagittatum.</i>
Ying yang huo (Yen yang ho) (China)	<i>E. sagittatum</i> , <i>E. grandiflorum</i> (as well as <i>Astilbe</i> sp. and <i>Thalictrum</i> sp. in drug markets), cf. pp. 414, 484, 508.

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and defining the species).

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EXPLANATION OF THE PLATES.

PLATE 24.—*Vancouveria hexandra* (Hook.) Morr. & Dene. (Type-specimen of *V. parvifolia* Greene. H. P. Chandler 1162 in U.S. Nat. Herb.); and *Vancouveria chrysanthra* Greene. (Co-type. Howell in Cons. Bot. Genève.)

PLATE 25.—*Vancouveria planipetala* Calloni. (Type-specimen of *V. concolor* Greene. Elmer 4922 in U.S. Nat. Herb.); and *Epimedium platypetalum* K. Meyer. (Co-type. Limpricht 1386 in Herb. Berlin.)

PLATE 26.—*Epimedium macrosepalum* Stearn. Specimens in herb. Bot. Institut, Akademii Nauk, Leningrad:—(1) Schischkin 1002; (2) Desoulavy 1049; (3) Desoulavy 3583 (type-specimen); (4) Kolesnikov 283; (5) drawing of flower of Desoulavy 3583 with inner sepal (below, left) and petal (below, right).

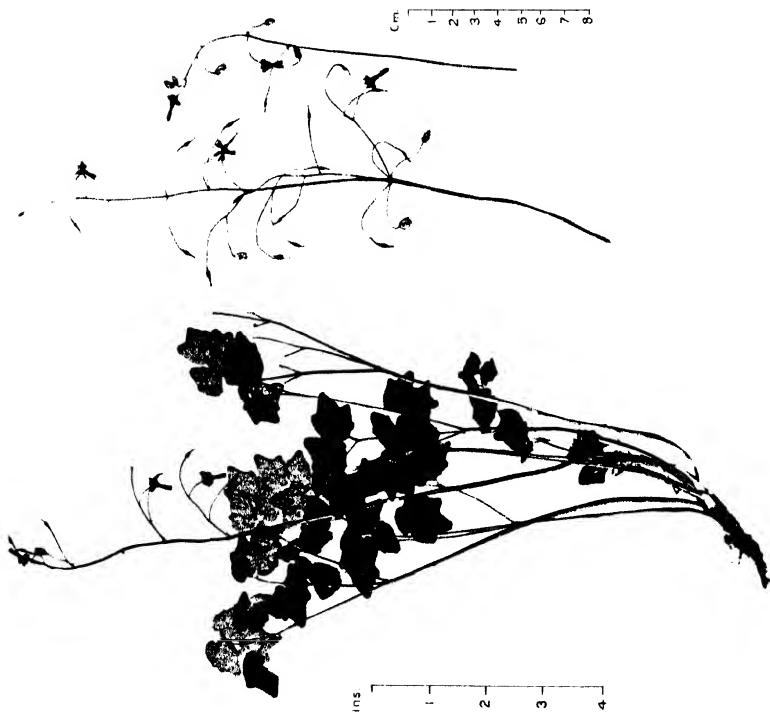
PLATE 27.—*Epimedium hunanense* (Hand.-Mazz.) Hand.-Mazz. (Type-specimen. Wang Te Hui 43 in Herb. Univ. Wien); and *Epimedium membranaceum* K. Meyer. (Type-specimen. Limpricht 1293 in Herb. Univ. Breslau.)

PLATE 28.—*Epimedium leptorrhizum* Stearn. (Type-specimen. Bodinier 2184 in Herb. Mus. Paris); and *Epimedium sutchuenense* Franch. (Type-specimen. Farges 1272 in Herb. Mus. Paris.)

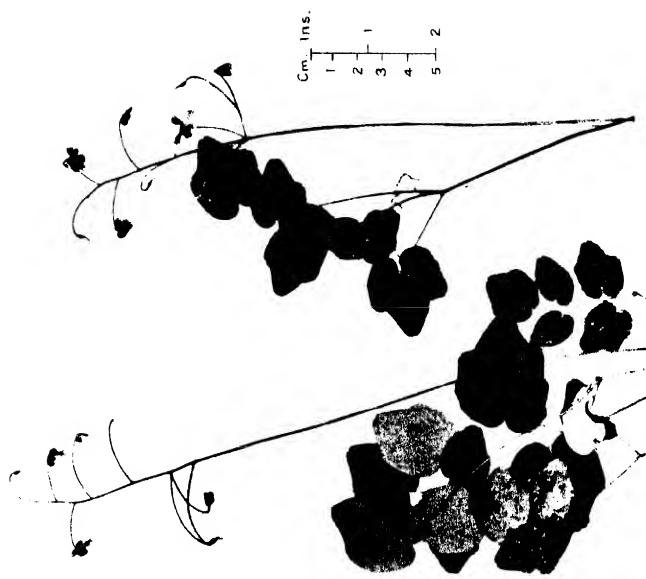
PLATE 29.—*Epimedium brevicornu* Max. (Co-types. Potanin in Herb. Edinburgh & Mus. Wien); and *Epimedium Fargesii* Franch. (Type-specimen. Farges 506 bis in Herb. Mus. Paris.)

PLATE 30.—*Epimedium pubescens* β *Cavaleriei* Stearn. (Authentic specimen from type-locality. Teng 0109 in Herb. Sun Yatsen Univ., Canton); and *Epimedium elongatum* Kom. (Stevens 196 in Herb. Berlin.)

PLATE 31.—1. *Epimedium grandiflorum* δ 'Rose-Queen' (Cult.) 2. $\times E. Youngianum$ α *typicum* Makino (Cult.) 3. $\times E. Youngianum$ β *roseum* (Vilm.-Andr.) Stearn. (Co-type of *E. concinnum* Vatke). 4. $\times E. Youngianum$ δ *niveum* (Vilm.-Andr.) Stearn. (Cult.). 5. Drawing of *Notsuzume-ikari* (four-fluked grapple) used by Japanese fishermen (cf. p. 483). 6. *E. diphylum* Lodd. (Cult.); and $\times E. versicolor$ δ *neo-sulphureum* Stearn. (Co-type. Herb. Kew.)



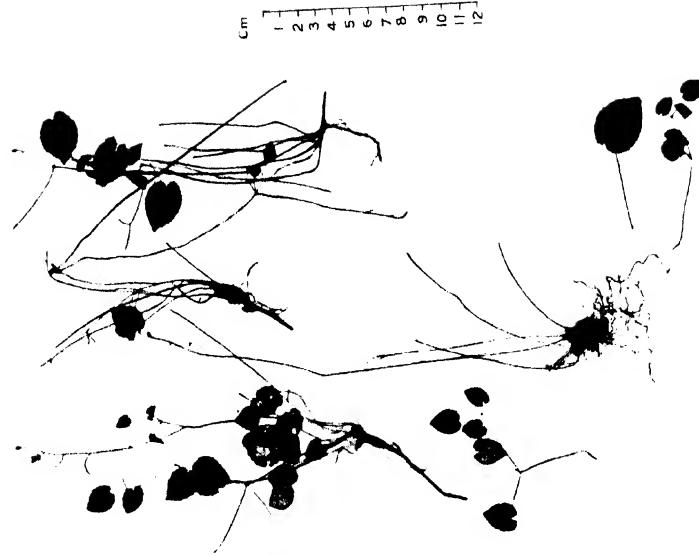
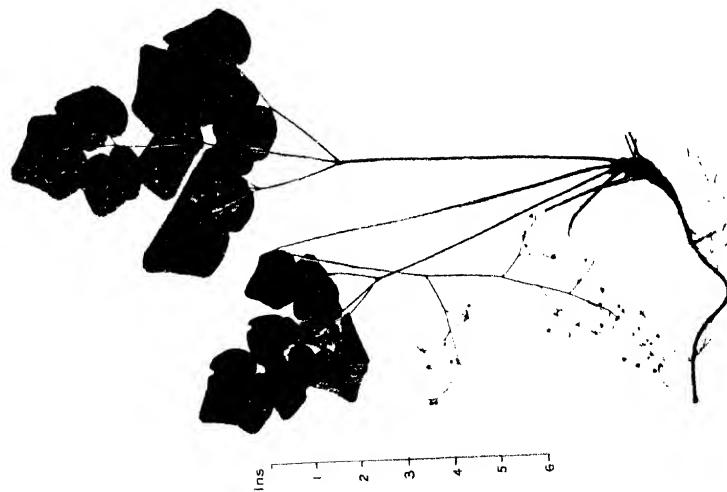
VANCOUVERIA HEXANDRA(HOOK.) MORR. & DCN.



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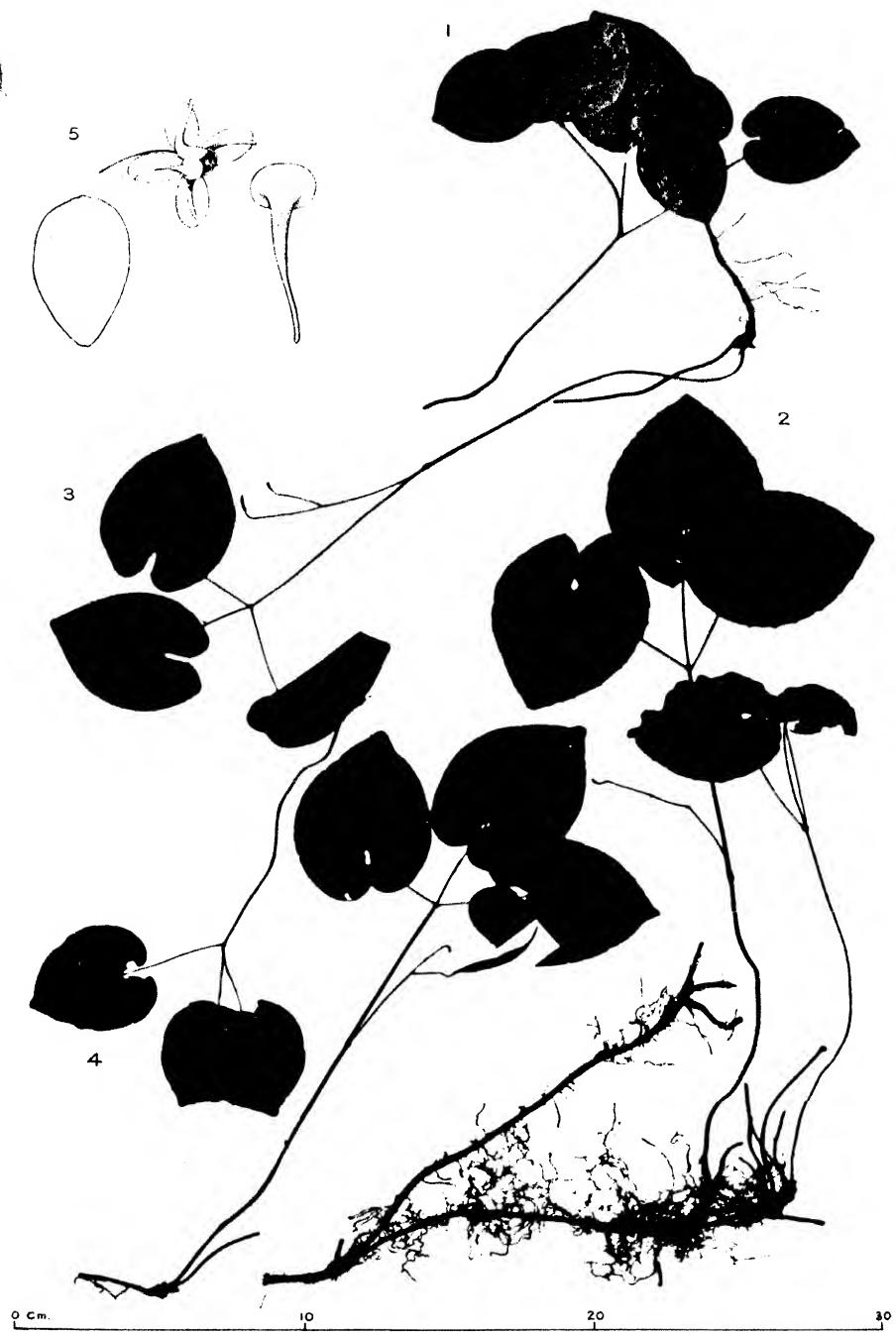
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VANCOUVERIA PLANIPETALA CALLIONI

EPIMEDIUM PLATYPETALUM K. MEYER.

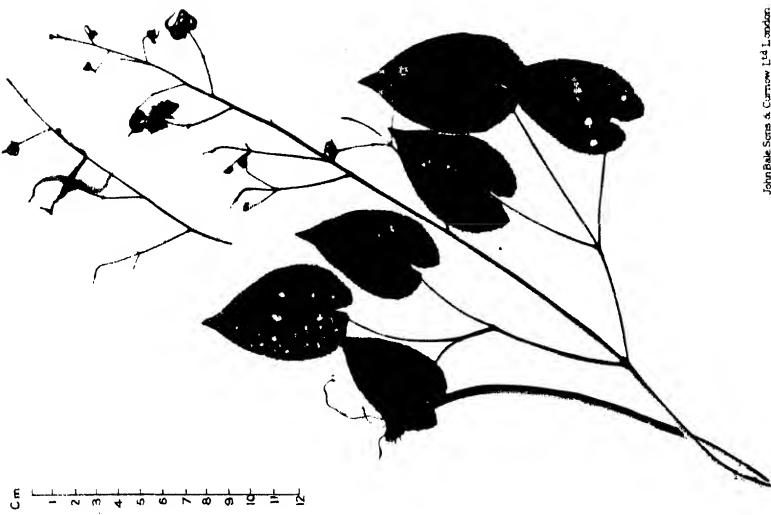


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EPIMEDIUM MACROSEPALUM STEARN.



EPIMEDIUM HUNANENSE HAND.-MAZZ.

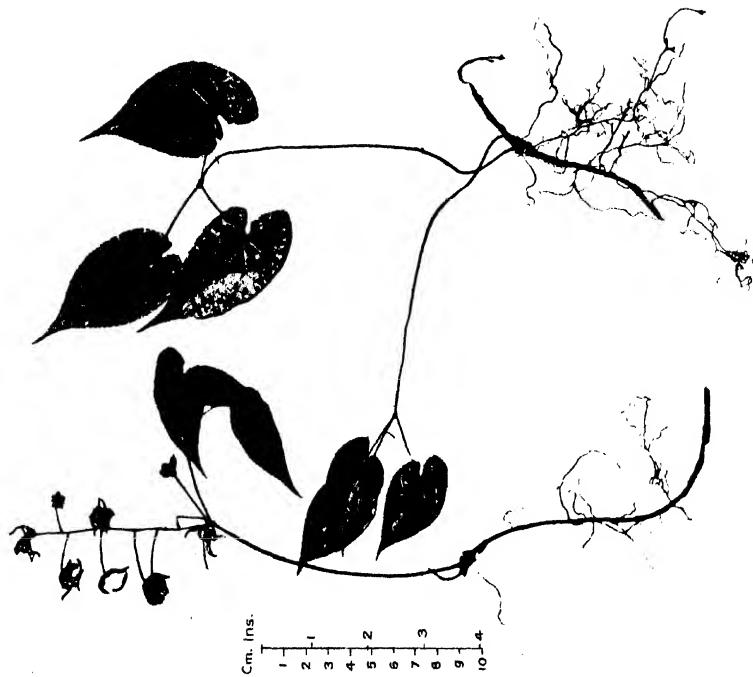


EPIMEDIUM MEMBRANACEUM K. MEYER.

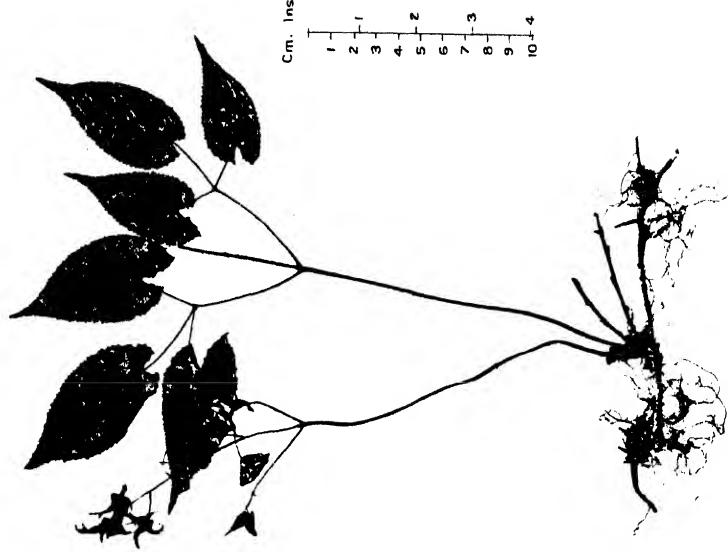
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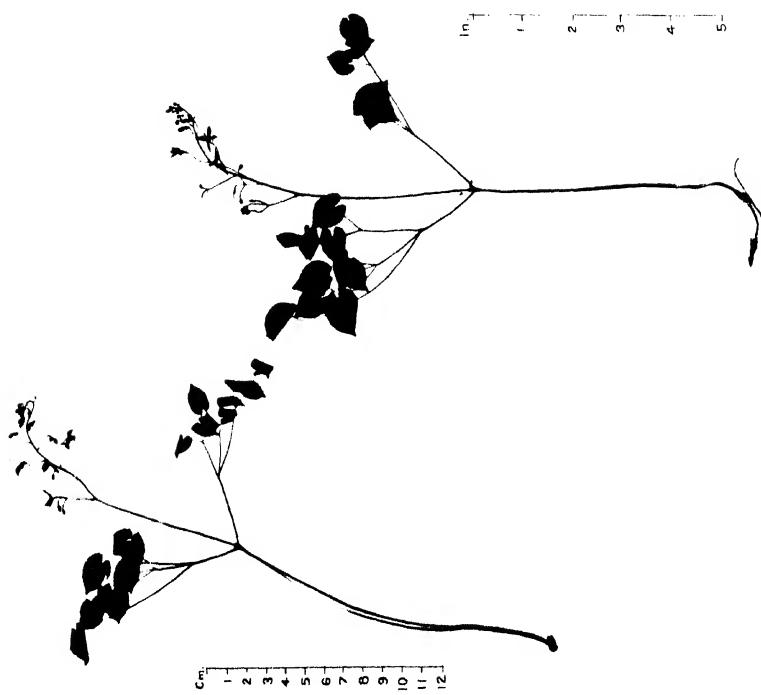


EPIMEDIUM LEPTORRHIZUM STEARN.

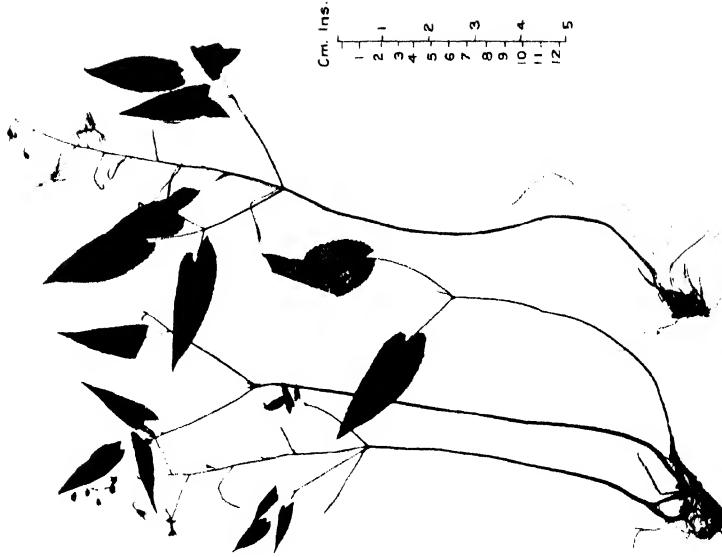


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EPIMEDIUM SUTCHUENSE FRANCH.



EPIMEDIUM BREVICORNU MAXIM.



John Bell Stearn & Currow 1:1 Septem.

EPIMEDIUM FARGESII FRANCH.

STEARN



EPIMEDIUM PUBESCENS β CAVALERIEI STEARN.

JOURN LINN. SOC., BOT. VOL. LI. PL. 30



EPIMEDIUM ELONGATUM KOM.

John East Society & Committee 1951 London



EPIMEDIUM DIPHYLLUM X E. GRANDIFLORUM

EPIMEDIUM VERSICOLOR & NEO-SULPHUREUM STEARN.

INDEX TO DESCRIPTIONS.

(Synonyms omitted. A star (*) denotes a name here published for the first time.)

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parietis mammillatis $25\text{--}35\mu$ altis circa 45μ latis. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, $52\text{--}60\times 20\text{--}23\mu$.

Hab. in foliis *Fici* sp., Lake Nabugabo, *Hansford* 2117 (leg. *P. Chandler*).

13. IRENINA HARUNGANAЕ Hansford, sp. nov. [3101.5330.]

Plagulae epiphyllae, tenues, atræ, 1–5 mm. diam., orbiculares. *Mycelium* ex hyphis brunneis rectiusculis $8\text{--}9\mu$ crassis septatis (articulis $35\text{--}50\mu$ longis) irregulariter ramosis anastomosantibus compositum. *Hyphopodia capitata* alternata, $32\text{--}36\mu$ longa, cellula basali cylindraceo-conoidea saepe curvata $10\text{--}15\mu$ longa, cellula apicali lobata $21\text{--}25\times 17\text{--}21\mu$. *Hyphopodia mucronata* sparsa, opposita, ampullacea. *Perithecia* aggregata in centro plagularum, globosa, atra, $180\text{--}220\mu$ diam., cellulis parietis conicis vel mammillatis circa 30μ altis et latis. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, $50\text{--}54\times 20\text{--}23\mu$.

Hab. in foliis *Harunganae madagascariensis*, Kisubi, Entebbe, *Hansford* 2295.

MELIOLA Fries.

69. MELIOLA AGELAEAE Hansford, sp. nov. [3113.4223.]

Plagulae epiphyllac, atræ, tenues, usque ad 3 mm. diam., velutinae. *Mycelium* ex hyphis brunneis rectiusculis $6\text{--}7\mu$ crassis opposite ramosis septatis (articulis $20\text{--}35\mu$ longis) compositum. *Hyphopodia capitata* opposita vel alternata, $17\text{--}20\mu$ longa, cellula basali cylindracea $3\text{--}6\mu$ longa, cellula apicali cylindracea curvata vel reflexa $11\text{--}16\times 7\text{--}9\mu$. *Hyphopodia mucronata* haud numerosa, sparsa. *Setae myceliales* numerosae, saepe juxta perithecia evolutae, $300\text{--}700\mu$ longae, basi $8\text{--}11\mu$ crassae, atræ, opacæ, rectæ, apice acutæ. *Perithecia* sparsa, globosa, atra, verrucosa, $160\text{--}200\mu$ diam. *Sporae* atro-brunneac, 4-septatae, cylindraceae, utrinque rotundatae, constrictae, $40\text{--}46\times 15\text{--}17\mu$.

Hab. in foliis *Agelaeae ugandensis*, Mile 13, Entebbe Road, *Hansford* 2275.

70. MELIOLA ARTABOTRYDIS Hansford, sp. nov. [311/31.6333.]

Plagulae amphigenae, densæ, 1–3 mm. diam., atræ, velutinac, rarius hypophyllæ majores et effusæ. *Mycelium* ex hyphis brunneis rectiusculis $8\text{--}10\mu$ crassis septatis (articulis $22\text{--}30\mu$ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata, $23\text{--}28\mu$ longa, cellula basali cylindracea $7\text{--}10\mu$ longa, cellula apicali oblonga vel curvata $15\text{--}19\times 10\text{--}14\mu$. *Hyphopodia mucronata* sparsa, ampullacea vel lageniformia, opposita. *Setae myceliales* erectæ, atræ, rectæ, $600\text{--}750\mu$ longae, basi $10\text{--}12\mu$ crassæ, apice acutiusculæ vel 2–5-dentatae (usque ad 9μ). *Perithecia* sparsa, atra, globosa, verrucosa, $190\text{--}230\mu$ diam. *Sporae* ellipsoideæ, atro-brunneæ, 4-septatae, constrictæ, $56\text{--}63\times 23\text{--}28\mu$.

Hab. in foliis *Artabotrydis nitidi*, Kisubi, Entebbe, *Hansford* 2296.

In this species the mucronate hyphopodia are much more numerous in some parts of the colonies than in others, as in *M. Xylopiae* Stevens, and the perithecia are situated on a basis of radiating hyphae, mostly non-hyphopodiæ but not forming a true disc.

71. **MELIOLA BORNEENSIS** Sydow in Ann. Myc., xxii, p. 90 (1923). [3111.5323.]
On *Popowia* (? *Maitlandii*), Kisubi, Entebbe, *Hansford* 2303.

72. **MELIOLA BUNYORENSIS** Hansford, sp. nov. [3111.5342.]

Plagulae amphigenae, plerumque epiphyllae, densae, atrae, crustosae, velutinae, orbiculares, usque ad 7 mm. diam., rarius confluentes et majores. *Mycelium* ex hyphis brunneis 7–10 μ crassis septatis (articulis 15–25 μ longis) undulatis opposite ramosis compositum. *Hyphopodia capitata* numerosissima, alternata, 18–35 μ longa, cellula basali cylindracea 6–14 μ longa, cellula apicali ovata clavata vel lobata 15–24 \times 10–21 μ . *Hyphopodia mucronata* in centro plagularum numerosa, inter hyphopodia capitata interspersa, opposita, ampullacea. *Setae myceliales* atrae, erectae, opacae, rectae, numerosae, 200–340 μ longae, basi 9–11 μ crassae, sursum attenuatae, rarius torulosae, apice acutae vel obtusae. *Perithecia* sparsa globosa atra verrucosa, 220–340 μ diam. *Sporae* atro-brunneae, ellipsoideae vel cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 47–53 \times 18–22 μ .

Hab. in foliis *Entandrophragmae angolensis*, Budongo Forest, *Hansford* 2309 (leg. W. J. Eggeling).

73. **MELIOLA BUSOGENSIS** Hansford, sp. nov. [3112.4222.]

Plagulae amphigenae, plerumque epiphyllae, orbiculares, atrae, velutinae, densae, 1–2 mm. diam. *Mycelium* ex hyphis brunneis rectiusculis 6–8 μ crassis septatis (articulis 15–20 μ longis) opposite ramosis compositum. *Hyphopodia capitata* opposita, 14–20 μ longa numerosa, cellula basali cylindracea 2–6 μ longa, cellula apicali clavata vel rotundata 10–13 \times 6–9 μ . *Hyphopodia mucronata* non visa. *Setae myceliales* numerosae, erectae, rectae, atrae, 250–400 μ longae, basi 8–10 μ crassae, sursum attenuatae, apice simplices sub-acutae vel acuminatae. *Perithecia* sparsa vel in centro plagularum aggregata, globosa, atra, verrucosa, 140–190 μ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 44–48 \times 17–19 μ .

Hab. in foliis *Jasmini* sp., Jinja, *Hansford* 2311 (leg. P. Chandler).

74. **MELIOLA CHAETACHMES** Hansford, sp. nov. [3131.5222.]

Plagulae hypophyllae, atrae, orbiculares, velutinac, densae sed non crustosae, usque 15 mm. diam. *Mycelium* ex hyphis brunneis undulatis 7–8 μ crassis septatis (articulis 25–45 μ longis) alternatim vel irregulariter rarius opposite ramosis compositum. *Hyphopodia capitata* alternata 22–32 μ longa, saepe curvata vel reflexa, cellula basali cylindracea 7–13 μ longa, cellula apicali clavata vel late rotundata 15–20 \times 9–15 μ . *Hyphopodia mucronata* inter hyphopodia capitata interspersa, opposita, plus minusve lageniformia, 20–24 μ longa, in collo curvato 3 μ crasso attenuata. *Setae myceliales* numerosissimae, erectae, atrae, rectae, opace atro-brunneae, 350–480 μ longae, basi 8–10 μ crassae, sursum attenuatae, apice acutae vel dentatae (usque ad 15 μ) saepe sursum sub-torulosae. *Perithecia* sparsa, atra, globosa, verrucosa, 140–160 μ diam. *Sporae* atro-brunneae, cylindraceae vel ellipsoideae, 4-septatae, constrictae, 54–59 \times 16–19 μ .

Hab. in foliis *Chaetachmes microcarpae*, Masaka Road, Mile 7, *Hansford* 2092.

75. *MELIOLA CHORLEYI* Hansford, sp. nov. [3133.4222.]

Plagulae hypophyllae, atrae, orbiculares, densae velutinae, usque ad 10 mm. diam. *Mycelium* ex hyphis brunneis undulatis 6–7 μ crassis septatis (articulis 25–45 μ longis) opposite ramosis anastomosantibus compositum. *Hyphopodia capitata* alternata vel opposita, saepe curvata, 14–20 μ longa, cellula basali cylindracea 3–7 μ longa, cellula apicali cylindracea vel ovata 8–14 \times 7–9 μ . *Hyphopodia mucronata* sparsa, haud numerosa, ampullacea, opposita. *Setae myceliales* numerosissimae, atrae, erectae, rectae, 200–400 μ longae, basi 7–8 μ crassae, apice 2–4-dentatae (usque ad 20 μ). *Perithecia* sparsa, atra, globosa, verrucosa, 150–190 μ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 42–47 \times 11–14 μ .

Hab. in foliis *Bersamae* sp., Entebbe Road Forests, *Hansford 2035* (leg. *T. Chorley & P. Chandler*).

The hyphopodia are often formed some little distance behind the septa of the parent hypha.

76. *MELIOLA DRACAENICOLA* Pat. & Har. in Bull. Soc. Myc. France, xxiv, p. 14 (1908).

Var. MAJOR Hansford, var. nov. [3141.5232.]

A typo ita differt:—*setae myceliales* numerosissimae, 200–340 μ longae, repetite dichotomae (rarius 3-furcatae), ramis usque ad 130 μ longis, ramulis secundariis usque 45 μ , tertiaris usque ad 35 μ et dentatis usque ad 10 μ ; ramis et ramulis late divaricatis. *Sporae* 45–51 \times 15–19 μ .

Hab. in foliis *Dracaenae fragrantis*, Entebbe Road, *Hansford 2046*.

77. *MELIOLA DUMMERI* Hansford, sp. nov. [3131.4231.]

Plagulae amphigenae, saepius epiphyllae, laxe vel dense sparsae, orbiculares vel effusae, usque ad 3 mm. diam., atrae, tenues vel densae. *Mycelium* ex hyphis brunneis undulatis 7–8 μ crassis septatis (articulis 17–35 μ longis) alternatim ramosis anastomosantibus compositum. *Hyphopodia capitata* alternata vel unilateralia, 16–22 μ longa, cellula basali cylindracea 3–8 μ longa, cellula apicali clavata vel sub-globosa saepe curvata vel reflexa 10–16 \times 9–13 μ . *Hyphopodia mucronata* haud numerosa opposita ampullacea, praecipue in centro plagularum evoluta. *Setae myceliales* numerosae, atrae, opacae, erectae, rectae, 200–280 μ longae, basi 7–9 μ crassae, apice 2–3-furcatae (usque ad 35 μ), ramis 2–5-denticulatis (usque ad 12 μ). *Perithecia* sparsa, atra, globosa, verrucosa, 130–180 (–240) μ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 37–42 \times 14–16 μ .

Hab. in foliis *Rhois incanae*, Entebbe Road, *Hansford 2265* (type).

In my previous paper (p. 275) *Dummer 1321*, which is now included here, was assigned to *M. geniculata* Syd. & Butl.; *Hansford 2012* also belongs to the present species, which differs from *M. geniculata* in the longer branches of the setae and from *M. brachydonta* Syd. in its distinctly furcate setae, though occasional setae are dentate only.

78. *MELIOLA GENICULATA* Syd. & Butl. in Ann. Myc. IX, p. 381 (1911).Var. *EGGELINGII* Hansford, var. nov. [3131.4221.]

Plagulae hypophyllae, tenues, effusae, atrae, confluentes. *Mycelium* ex hyphis brunneis undulatis 6–7 μ crassis septatis (articulis 30–55 μ longis) opposite ramosis anastomosantibus compositum. *Hyphopodia capitata* alternata, 15–22 μ longa, cellula basali cylindracea saepe reflexa 5–8 μ longa, cellula apicali ovata vel oblonga 10–15 \times 7–10 μ . *Hyphopodia mucronata* inter hyphopodia capitata interspersa, opposita, ampullacea. *Setae myceliales* numerosae, erectae, rectae, atrae, 240–280 μ longae, basi 6–9 μ crassae, apice sub-pellucidae, 2–6-dentatae vel breviter furcatae (usque ad 13 μ), cristatae. *Perithecia* sparsa, globosa, atra, verrucosa, 140–180 μ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 38–43 \times 14–18 μ .

Hab. in foliis *Entandrophragmae angolensis*, Budongo Forest, Hansford 2307 (leg. W. J. Eggeling).

Differs from the type chiefly in less numerous hyphopodia and larger spores, and from *M. brachydonta* Syd. in the epiphyllous colonies, opposite branches of the mycelium, and scattered perithecia. Only a few colonies are present on this material.

79. *MELIOLA HARRISONIAE* Hansford, sp. nov. [3113.3221.]

Plagulae epiphyllae, 0.5–1 mm. diam., atrae, tenues, orbiculares. *Mycelium* ex hyphis brunneis rectiusculis septatis (articulis 17–30 μ longis) 6 μ crassis opposite ramosis compositum. *Hyphopodia capitata* alternata vel opposita, saepius alternata, 12–14 μ longa, cellula basali breviter cylindracea 3–5 μ longa, cellula apicali ovata 8–11 \times 7–9 μ . *Hyphopodia mucronata* haud numerosa, inter hyphopodia capitata interspersa, ampullacea. *Setae myceliales* praeccipue juxta perithecia evolutae, 180–240 μ longae, atrae, basi 7–9 μ crassae, sursum ad apicem obtusum sub-pellucidum sensim attenuatae. *Perithecia* sparsa, atra, globosa, verrucosa, 140–180 μ diam. *Sporae* atro-brunneae, cylindraceae utrinque rotundatae, 4-septatae, constrictae, 34–39 \times 13–15 μ .

Hab. in foliis *Harrisoniae abyssinicae*, Entebbe Road, Hansford 2014.

80. *MELIOLA INTERMEDIA* Gaill. in Le Genre *Meliola* p. 94 (1892). [311/21. 4232.]

On *Apocynacearum* sp. indet., Hansford 1975, Mukono Forest, Kiagwe.

81. *MELIOLA JUSTICIAE* Hansford, sp. nov. [3133.3223.]

Plagulae epiphyllae, numerosae, densae, atrae, usque ad 1.5 mm. diam. *Mycelium* ex hyphis brunneis 6–7 μ crassis undulatis septatis (articulis 13–20 μ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata vel opposita, numerosa, 13–17 μ longa, cellula basali cylindraceo-conoidea 3–6 μ longa, cellula apicali late rotundata vel sub-globosa 8–11 μ diam. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, haud numerosa, ampullacea. *Setae myceliales* numerosae, atrae, erectae, rectae, 180–580 μ longae, basi 9–11 μ crassae, apice furcatae vel dentatae (usque ad 10 μ). *Perithecia* sparsa,

globosa, atra verrucosa, $80-160\mu$ diam. *Sporae* atro-brunneae, cylindraceae vel ellipsoideae, utrinque rotundatae, 4-septatae, constrictae, $34-39\times 12-15\mu$.

Hab. in foliis *Justiciae* (? *laxae*), Masaka Road, *Hansford 2013*.

82. MELIOLA KHAYAE Hansford, sp. nov. [3133.5231.]

Plagulae amphigenae, atrae, densae, velutinae, orbiculares, usque ad 5 mm. diam. *Mycelium* ex hyphis undulatis brunneis $7-9\mu$ crassis septatis (articulis $17-35\mu$ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata vel opposita $18-28\mu$ longa, cellula basali cylindracea curvata $6-7\mu$ longa, cellula apicali cylindracea vel clavata $15-20\times 8-10\mu$. *Hyphopodia mucronata* non visa. *Setae myceliales* erectae, atrae, rectae, usque ad 260μ longae, basi $8-10\mu$ crassae, apice 2-3-furcatae (usque ad 40μ), ramis dentatis (usque ad 15μ). *Perithecia* sparsa, atra, globosa, verrucosa, $180-320\mu$ diam. *Sporae* cylindraceae, utrinque rotundatae, atro-brunneae, 4-septatae, constrictae, $48-56\times 19-22\mu$.

Hab. in foliis *Khayae antothecae*, Budongo Forest, *Hansford 1991* (leg. R. G. Sangster) (type); *Hansford 2308* (leg. W. J. Eggeling).

83. MELIOLA LANDOLPHIAE-FLORIDAE Hansford, sp. nov. [3111.4223.]

Plagulae epiphyllae, atrae, orbiculares, tenues, usque ad 10 mm. diam. *Mycelium* ex hyphis brunneis rectis $6-8\mu$ crassis septatis (articulis $25-35\mu$ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata $24-30\mu$ longa, cellula basali cylindraceo-conoidea $4-9\mu$ longa, cellula apicali ovata vel clavata $17-22\times 9-11\mu$. *Hyphopodia mucronata* sparsa, opposita, ampullacea. *Setae myceliales* haud numerosae, praecipue juxta perithecia evolutae, erectae, atrae, rectae, $350-520\mu$ longae, basi $7-9\mu$ crassae, sursum ad apicem obtusum attenuatae. *Perithecia* sparsa, atra, globosa, verrucosa, $120-150\mu$ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, $37-40\times 15-17\mu$.

Hab. in foliis *Landolphiae floridæ*, Kazi near Kampala, *Hansford 2324*.

84. MELIOLA LORANTHI Gaill. in Le Genre *Meliola*, p. 105 (1892). [3133.6322.]

On *Loranthus* sp., Lake Nabugabo, *Hansford 2110* (leg. P. Chandler).

85. MELIOLA MONODORAE Hansford, sp. nov. [3111.3221.]

Plagulae epiphyllae, tenues, effusae, atrae. *Mycelium* ex hyphis brunneis rectiusculis vel leniter undulatis 7μ crassis septatis (articulis $20-35\mu$ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata, $16-24\mu$ longa, cellula basali cylindracea $5-7\mu$ longa, cellula apicali late rotundata vel sub-globosa $12-15\times 10-12\mu$. *Hyphopodia mucronata* sparsa, opposita, ampullacea, recta vel curvata. *Setae myceliales* sparsae, praecipue juxta perithecia evolutae, rectae vel curvatae, $140-220\mu$ longae, basi $6-8\mu$ crassae, atrae, apice obtusae. *Perithecia* sparsa, globosa, atra, verrucosa, $150-180\mu$ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, $35-40\times 13-16\mu$.

Hab. in foliis *Monodora* *Gibsonii*, Budongo Forest, Eggeling 3066 (Hansford 2243).

This differs from *M. Popowiae* Doidge in the much shorter setae, which are never swollen at the tip, and in the hyphae and capitate hyphopodia.

86. **MELIOLA NYANZAE** Hansford, sp. nov. [3113.3222.]

Plagulae epiphyllae et caulicolae, atrae, orbicularis, velutinae, usque 10 mm. diam. *Mycelium* ex hyphis undulatis 6–9 μ crassis septatis (articulis ad 23–40 μ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata vel opposita 15–20 μ longa, cellula basali cylindracea, saepe curvata, 4–8 μ longa, cellula apicali sub-globosa vel clavata, saepe reflexa, 10–16 \times 10–15 μ . *Hyphopodia mucronata* opposita, ampullacea collo recto vel curvato. *Setae myceliales* numerosae, atrae, erectae, rectae, 240–330 μ longae, basi 6–10 μ crassae, sursum attenuatae, apice sub-acutae vel acuminatae, rarius obtusae. *Perithecia* sparsa, globosa, atra, verrucosa, 130–170 μ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 31–37 \times 10–13 μ .

Hab. in foliis *Indigoferae* sp., Jinja, Hansford 2312 (leg. P. Chandler).

The colonies are dense and towards the centre the mycelium and hyphopodia form almost a solid plate; the mucronate hyphopodia are formed on separate hyphae.

87. **MELIOLA OLIGOMERA** H. & P. Sydow in Ann. Myc. xv, p. 190 (1917). [2121.4221.]

On an unknown host, Masaka Road, Mile 7, Hansford 2093. The setae in this material are somewhat bent, and thus differ from Stevens's account (in Ann. Myc. xxvi, p. 166; 1928).

88. **MELIOLA POLYTRICHA** Kalchbr. & Cooke in Grevillea, 1880, p. 72. [3111.5221.]

On *Pittosporum abyssinicum*, near Kampala, Hansford 1987; Lake Nabugabo, Hansford 2083 (leg. P. Chandler); Entebbe Road, Hansford 2289. The setae in most colonies do not exceed 280 μ , but otherwise the specimens agree with the description given by Doidge (in Bothalia, II, p. 458).

89. **MELIOLA PYCNOTACHYDIS** Hansford, sp. nov. [3133.3221.]

Plagulae amphigenae, plerumque epiphyllae, densae velutinae, atrae. *Mycelium* ex hyphis brunneis undulatis 6–7 μ crassis septatis (articulis 18–30 μ longis) opposite ramosis anastomosantibus compositum. *Hyphopodia capitata* alternata vel opposita, numerosa, 11–16 μ longa, cellula basali cylindracea 2–5 μ longa, cellula apicali globosa vel ovata 7–12 μ diam. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, opposita, ampullacea. *Setae myceliales* numerosae, erectae, rectae, atrae, 180–260 μ longae, basi 7–8 μ crassae, apice 2–3-furcatae vel dentatae (usque ad 20 μ). *Perithecia* sparsa, atra,

globosa, verrucosa, $130\text{--}160\mu$ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, $32\text{--}37\times 12\text{--}14\mu$.

Hab. in foliis *Pycnostachydis* sp., Entebbe Road Forest, *Hansford 2100* (leg. *P. Chandler*).

90. *MELIOLA RAMICOLA* Hansford, sp. nov. [3113.4231.]

Plagulae caulicolae, atrae, velutinae, densae, usque ad 4 mm. diam. *Mycelium* ex hyphis brunneis rectiusculis $7\text{--}10\mu$ crassis septatis (articulis $15\text{--}35\mu$ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata vel opposita, numerosissima, $17\text{--}25\mu$ longa, cellula basali cylindracea $2\text{--}6\mu$ longa, cellula apicali rotundata vel sub-globosa $11\text{--}19\times 11\text{--}17\mu$. *Hyphopodia mucronata*, opposita, lageniformia, praecipue in centro plagularum evoluta. *Setae myceliales* numerosae, atrae, erectae, rectae, opacae, crasse tunicatae, $170\text{--}240\mu$ longae, basi $10\text{--}14\mu$ crassae, versus apicem acutum vel sub-acutum attenuatae, simplices. *Perithecia* sparsa, globosa, atra, verrucosa, $180\text{--}220\mu$ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae constrictae, $46\text{--}49\times 16\text{--}18\mu$.

Hab. in cortice ramulorum *Uvariae Welwitschii*, Kazi near Kampala, *Hansford 2316*.

No colonies were found on the leaves of this material, and the fungus is restricted to the bark of twigs one year old; the mycelium and capitate hyphopodia form almost a solid plate.

91. *MELIOLA SAKAWENSIS* P. Henn. in *Hedwigia*, XLIII, p. 141 (1904).

Var. *MAJOR* Hansford, var. nov. [3111.4232.]

A typo ita differt:—*Sporae* $37\text{--}45\times 13\text{--}15\mu$. *Perithecia* $170\text{--}250\mu$ diam.

Hab. in foliis *Lantanae* spec., Kinkizi Gorge, alt. 4,500 ft., Kigezi, *Hansford 2151*.

92. *MELIOLA SCLEROCHITONIS* Hansford, sp. nov. [311/31.4222.]

Plagulae amphigenae, plerumque epiphyllae, atrae, velutinae, orbicularis, usque ad 2 mm. diam. *Mycelium* ex hyphis brunneis undulatis $6\text{--}8\mu$ crassis septatis (articulis $15\text{--}28\mu$ longis) opposite ramosis compositum. *Hyphopodia capitata* alternata vel unilateralia, numerosa, $13\text{--}18\mu$ longa, cellula basali cylindracea $3\text{--}5\mu$ longa, cellula apicali globosa $11\text{--}14\mu$ diam. *Hyphopodia mucronata* inter hyphopodia capitata interspersa, lageniformia. *Setae myceliales* numerosae, atrae, erectae, rectae, $280\text{--}400\mu$ longae, basi $8\text{--}10\mu$ crassae, apice acutae vel 2-3-dentatae (usque ad 10μ). *Perithecia* sparsa, globosa, atra, verrucosa, $120\text{--}160\mu$ diam. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, $39\text{--}42\times 12\text{--}15\mu$.

Hab. in foliis *Sclerochitonis obtusisepali*, Masaka Road, Mile 7, *Hansford 2001, 2256*.

Hansford 1495 from Mile 10, Toro Road, appears to be this species, probably on the same host,

93. **MELIOLA SUBSTENOSPORA** von Hoehnel in Sitzber. K. Akad. Wiss. Wien, Math.-natur. Kl., cxviii, p. 317 (1909). [3111.4223.]

On *Olyra latifolia*, Entebbe Road Forest, *Hansford* 2088 (leg. *P. Chandler*). The setae in this material are longer than recorded by Stevens (Ann. Myc. xxvi, p. 283 ; 1928) and reach 600μ .

94. **MELIOLA THUNBERGIAE** Hansford, sp. nov. [3111.4221.]

Plagulae amphigenae, orbiculares, atrae, densae, velutinae, 1–4 mm. diam., non crustosae. *Mycelium* ex hyphis brunneis $6\text{--}8\mu$ crassis rectiusculis septatis (articulis $21\text{--}40\mu$ longis) alternatim ramosis compositum. *Hyphopodia capitata* alternata, $22\text{--}32\mu$ longa, cellula basali conoidea saepe curvata $8\text{--}14\mu$ longa, cellula apicali ovata $14\text{--}19\times 10\text{--}15\mu$. *Setae myceliales* numerosae, rectae vel curviusculae, erectae, atrae, $200\text{--}300\mu$ longae, basi 10μ crassae, apice obtusae. *Perithecia* globosa, atra, verrucosa, $140\text{--}190\mu$ diam., in centro plagularum aggregata. *Sporae* atro-brunneae, cylindraceae, utrinque rotundatae, 4-septatae constrictae, $38\text{--}44\times 16\text{--}18\mu$.

Hab. in foliis *Thunbergiae alatae*, Mile 9, Masaka Road, *Hansford* 2252.

This species is close to *M. Psychotriæ* Earle, but has larger spores.

95. **MELIOLA UNCIATA** Syd. in Leafl. Philippine Bot., ix, 3120 (1925). [3121.4221.]

On *Pycnanthus* sp., Mile 13, Entebbe Road, *Hansford* 2181. This specimen differs from the type as described by Stevens (Ann. Myc. xxvi, p. 213 ; 1928) in its thin colonies and in the mycelial setae, which are in most cases only slightly bent.



A Florula of the island of Espiritu Santo, one of the New Hebrides. By A. GUILLAUMIN, Professor at the Muséum national d'Histoire Naturelle, Paris; with a prefatory note by the Leader of the Oxford University Expedition to the New Hebrides, 1933-34—JOHN R. BAKER. (Communicated by the PRESIDENT.)

[Read 5 May 1938]

THE collection of plants described below was made from October 1933 to February 1934 by Miss Ina Baker with the assistance of Mrs. Zita Baker, members of the Oxford University Expedition to the New Hebrides. The expedition was under the auspices of the Oxford University Exploration Club, and was supported by the Royal Society, the Royal Geographical Society, the Percy Sladen Trust and the British Museum (Natural History). The main objects of the expedition were (1) to study seasonal phenomena in animals and plants in a climate which varies very little during the year and (2) to explore the previously unknown region of Mt. Tabwemasana (6195 feet), the highest mountain in the New Hebrides.

The New Hebrides are situated in the southern tropics of the Western Pacific Ocean, to the north-east of New Caledonia. The collection of plants was made in Espiritu Santo, the largest island of the group. This island is a little less than 70 miles long by 40 broad. It is situated about 15° S. of the equator. The natural vegetation, which is nearly everywhere a luxuriant tropical rain-forest of rather small trees, covers much the greater part of the island, but there are large grassy patches on the northern slopes of the mountains in the vicinity of Mt. Tabwemasana in the west of the island. The climate is always hot except in the mountains, the rainfall is heavy, and over a large part of the island there is no true dry season. A full description of the climate will be found in Baker and Harrison (1936), and an account of some aspects of the botany in Baker and Baker (1936).

Hog harbour, in whose vicinity most of the plants were collected, is on the east side of the island. The rock in this district is upraised coral. The mountains of the western part of the island are largely of basic volcanic rocks. A note on the geology of the island, together with a general account of the expedition's activities, may be found in Baker (1935).

In what follows the native names for places and plants are spelled in accordance with the Royal Geographical Society's system No. 2. Briefly, the consonants are given their English values, except that the soft 'th' of 'this' (as opposed to its hard sound in 'thick') is written 'dh'. The vowels are Italian, except that the French "u" is written "ü" and the indefinite sound of the 'e' in the French 'le' is written 'ë'.—JOHN R. BAKER.

Although the island of Espiritu Santo is the largest of the New Hebrides, the flora is known only from the collections made by the Rev. F. A. Campbell in 1872-3 (Mueller, 1873), by Quaife in 1902 (Ames, 1933, and Rolfe, 1909, and Schlechter, 1912), of the Sydney University Expedition to the South Sea islands under the auspices of Captain Rason, and by Mr. and Mrs. Aubert de la Rue in 1934 (Guillaumin, 1935).

Campbell gathered 18 species : *Sida rhombifolia*, *Hibiscus Abelmoschus*, *Grewia Malococca*, *Evodia hortensis*, *Murraya exotica*, *Ervatamia orientalis*, *Hemigraphis reptans*, *Ocimum Basilicum*, *O. sanctum*, *Coleus scutellarioides*, *Euphorbia hirta*, *E. hypericifolia*, *Boehmeria platyphylla*, *Corymborchis vera-trifolia*, *Guillainia neo-ebudica*, *Scleria margaritifera*, *Oplismenus compositus*, and *Cenchrus calyculatus*. Quaife added 2 Orchids : *Dendrobium Quaifei* (Ames, 1933) and *Stauropsis Quaifei* (Rolfe, 1909, and Schlechter, 1912) ; Aubert de la Rue, 8 species : *Acacia spirorbis*, *Passiflora foetida*, *Vernonia cinerea*, *Ageratum conyzoides*, *Excavatia neo-ebudica*, *Clerodendron inerme*, *Amaranthus hypochondriacus*, and *Spathoglottis Petri*.

In a recent paper, John R. and I. Baker (1936) cited 13 plants, of which 12 had not been recorded from the island : *Alphitonia zizyphoides*, *Erythrina indica*, *Castanospermum australe*, *Pterocarpus indicus*, *Garuga floribunda*, *Spondias dulcis*, *Eugenia* sp., *Barringtonia samoensis*, *Terminalia Catappa*, *Geophila herbacea*, *Psychotria* sp., *Piper methysticum*, and *Ficus copiosa*, collected at Hog harbour.

Therefore the great interest of the collection made by Miss Ina Baker with the assistance of Mrs. Zita Baker, and preserved in the British Museum of Natural History. Unfortunately the specimens are frequently too imperfect for the determination to be certain.

DILLENIACEAE.

DILLENNIA NEO-EBUDICA Guillaum.—Hog harbour, rain forest ; shrub, 10 ft. ; *Tavoni* ; (286) 25. i. 34.

ANNONACEAE.

CANANGIUM ODORATUM (Lam.) Baill. ex King.—Hog harbour, rain forest ; tree, petals yellow ; *Nariüs* ; (69) 27. xi. 33 : (69 a) 24. i. 34.

ANNONA MURICATA Linn.—Hog harbour, rain forest ; tree ; *Nidhia nerur* ; (317) 2. ii. 34.

A. RETICULATA Linn.—Hog harbour, rain forest ; *Nidhia* ; (204) 21. i. 34 : *Nedhia nera* ; (309), not indigenous ; 2. i. 34.

CRUCIFERAE.

CARDAMINE SARMENTOSA Forst. f.—Hog harbour, in a path ; (178) 13. i. 34.

BIXACEAE.

BIXA ORELLANA Linn.—Hog harbour, rain forest ; seeds used by natives for staining hair and face red ; *Népekara* ; (218) 24. i. 34.

FLACOURTIACEAE.

PANGIUM sp.—perhaps **P. EDULE** Reinw.—Hog harbour, rain forest ; tree, white flowers, 2 sepals, 5 petals, fleshy stamens, large brown berry with yellow flesh, 6 inches ; *Nevagh* ; (273) 26. i. 34.

PORTULACACEAE.

PORTULACA OLERAcea Linn.—Hog harbour, open fields ; yellow flowers ; (114) 13. i. 34.

MALVACEAE.

URENA LOBATA Linn.—Hog harbour ; *Nèapsara* ; (82) 6. xii. 33 *.

HIBISCUS ABUTILOIDES Willd.—Hog harbour, rain forest ; yellow flowers, wild Cotton ; *Nèvehu* ; (248) 24. i. 34.

H. ROSA-SINENSIS Linn.—Hog harbour, garden ; a horticultural form with double yellow flowers ; (197 pro parte) 14. i. 34 : Tungwi, garden ; yellow flowers ; (159) 29. xii. 33.

SIDA RHOMBIFOLIA Linn.—Hog harbour, rain forest ; herb, yellow flowers ; *Nweding irin irin* ; (48) 20. xi. 33.

STERCULIACEAE.

STERCULIA sp.—Without locality ; brownish berry containing large seeds *Nalke* ; (257).

KLEINHOVIA HOSPITA Linn.—Hog harbour, rain forest ; tree, pink flowers *Néntal* ; (68) 27. ii. 33.

TILIACEAE.

GREWIA MALOCCCA Linn. f.—Hog harbour, rain forest ; *Nekos* ; (94) 10. xii. 33.

MALPIGHIACEAE.

RYSOPTERYS DISCOLOR Gandoger forma **STIPULACEA** Niedenzu.—Hog harbour, rain forest ; climber ; *Nuihiyara* ; (225) 24. i. 34.

OXALIDACEAE.

OXALIS CORNICULATA Linn.—Hog harbour, field near hedge ; yellow flowers ; (175) 13. i. 34 : Mt. Tabwemasana, 4,000 feet, open grassland ; small plant, yellow flowers ; (33) 29. x. 33.

BALSAMINACEAE.

IMPATIENS BALSAMINA Linn.—Tungwi, garden ; red flowers ; (161) 27. xii. 33.

RUTACEAE.

EVODIA HORTENSIS Forst.—Hog harbour, rain forest ; white flowers ; *Nörau* ; (65) 27. ii. 33 : Hog harbour, rain forest ; unpleasant smell ; (283) 27. i. 34.

* With this species agrees the incomplete sheet : Tanna (Kajewski, no. 180), which I enumerated (*Journ. Arn. Arb.* xii, p. 231, 1931) under *Triumphetta*.

E. SCHULLEI Warb. var. SIMPLICIFOLIA Guillaum.—Tungwi, garden ; shrub, yellow flowers ; (157) 29. x. 33 ; Hog harbour, garden ; very unpleasant smell, white flowers, yellow leaves ; (187) 15. i. 34.

E. TRIPHYLLOides DC.—Hog harbour, rain forest ; green berries ; *Rovhedhem* ; (240) 24. i. 34.

MURRAYA EXOTICA DC.—Hog harbour, rain forest ; *Napudhlan* ; (219) 24. i. 34.

MICROMELUM PUBESCENS Bl.—Hog harbour ; cymose inflorescence of small white flowers ; (207) 21. i. 34.

SIMARUBACEAE.

SOULAMEA AMARA Lam.—Hog harbour ; shrub, strand ; *Nea-yara* ; (227) 24. i. 34. Formerly only known from the Admiralty Islands to the west.

BURSERACEAE.

GARUGA FLORIBUNDA Dcne.—Hog harbour, rain forest ; deciduous tree ; *Nalü* ; (2) 19. i. 34.

MELIACEAE.

DYSOXYLUM BAKERARUM Guillaum., sp. nov.—*Rami* ? foliis glaberrimis, foliolis 17 (?) alternis sessilibus linear-lanceolatis (13–14 cm. × 3–4 cm.) basi valde asymmetricis uno latere rotundatis altero anguste cuneatis apice valde obtusis aliquando acutis. Panicula longa, ultra 30 cm. longa, glaberrima, ramis usque ad 11 cm. longis, floribus sessilibus 1 cm. longis. *Sepala* 5, libera, ovata, apice rotundata, extra appresse pilosa, intus glabra, 3 mm. longa. *Petala* extra appresse pilosa, intus glabra. *Tubus stamineus* 6 mm. longus, infra medium liber et extra hirsutus, margine laciniatus, laciinis in utraque pagina glabris : antherae 10, anguste ovatae, 1 mm. longae, e tubo stamineo leviter exsertae, basi insertae, glabrae. *Disci* tubus 5 mm. longus, glaberrimus, margine 5-crenulatus. *Ovarium* fulvum, hirsutum, 8 mm. longum, in stylum fulvum hirsutum sensim attenuatum, stigmate discoideo 5-crenulato.

Hog harbour, rain forest ; *Naspyü* ; (100) 11. ii. 33. Reminds one in appearance of *D. decandrum* Merr. (= *Turraea decandra* Blanco), but is very distinct by the alternate, more linear leaflets.

D. sp.—Hog harbour, rain forest ; *Nütbero* ; (19) 6. xii. 33.

D. sp.—Hog harbour, 90 ft., rain forest ; *Napüth* ; (22) 11. xi. 33.

MELIA AZEDARACH Linn.—Hog harbour, rain forest ; *Nësida* ; (60) 24. xi. 33.

VAVAEA SCAEVOLOIDES Guillaum., sp. nov.—*Frutex*. *Folia* obovata, usque ad 16 cm. × 6 cm., petiolo 1–2 cm. longo minute puberulo ; lamina basi acuta, apice breviter acuminata, supra costa nervisque exceptis glabra, subtus sparse hirsuta, nervis 10–11-jugis subtus prominentibus, venis dense reticulatis. *Inflorescentiae* ad ramulorum apicem axillares, corymbose paniculatae, 7–10 cm. longae, pedunculo 5–6 cm. longo breviter hirsuto, bracteis ellipticis (2 cm. × 0.5 cm.) distincte petiolatis supra glabrescentibus subtus praesertim marginibus et costa hispidis, bracteolis subulatis hispidis, pedicello 3 mm. longo hispido. *Calyx* 4–5-partitus, lobis inaequalibus ovatis apice rotundatis nervosis extra

hirsutis intus glabris. *Petala* 4–5, spathulata, extra apicem versus carinata, minute puberula, intus basi excepta minute puberula. *Stamina* 8–10, filamentis in tubum connatis, tubo usque ad medium discoideo incrassatoque apice intus extraque dense barbato; antherae oblongae, glabrae. *Ovarium* hirsutum, 4–5-loculare, stylo ovario longiore, stigmate discoideo.

Hog harbour; large shrub; *Neswnamal*; (236) 24. i. 34.

Seems especially near *V. Chalmersii* C. DC. of New Guinea.

RHAMNACEAE.

ALPHITONIA ZIZYPHOIDES A. Gray.—Near Hog harbour, 350 ft.; *Nowerié*; (4) 15. xi. 33. This is the tree whose fruiting gives the signal for the planting of sweet potatoes.

AMPELIDACEAE.

CAYRATIA CARNOSA (Lam.) Gagnep.—Hog harbour, rain forest; *Nwaékara*; (14) 9. xii. 33.

C. CARNOSA (Lam.) Gagnep. ?—Hog harbour, rain forest; 90 ft.; (14 a) 30. x. 34.

C. SAPONACEA Dom.—Hog harbour, rain forest; climber, serrate leaves, white berries; (307) 1. ii. 34.

LEEA SAMBUCINA Willd.—Hog harbour, rain forest; *Néherher*; (73) xii. 33; (80) 6. xii. 33; (80 a) 24. i. 34.

SAPINDACEAE.

CARDIOSPERMUM HALICACABUM Linn.—Hog harbour; yellow flowers; *Nwoiserio*; (109) 20. xii. 33.

ALLOPHYLLUS TERNATUS (J. R. & G. Forst.) Radlk.—Lowerie, between garden and bush; *Del-del*; (125) 27. xii. 33, red berries; Hog harbour, rain forest; *Nédrelrel*; (107) xii. 33; *Nédran*; (289) 27. i. 34.

A. TIMORENSIS Bl.—Hog harbour, rain forest; bush, spikes of white flowers; *Relrel*; (235) 24. i. 34.

POMETIA PINNATA J. R. & G. Forst.—Hog harbour, rain forest; buttress roots; *Neseli*; (325) 2. ii. 34; *Neseli*; (215) 23. i. 34.

ANACARDIACEAE.

SPONDIAS DULCIS Forst. f.—Hog harbour, rain forest; *Nü*; (202) 20. i. 34. Said by natives to be deciduous and shed its leaves at the same time as *Nalü*, i.e. *Garuga floribunda*.

RHUS RETUSA Zoll.—Hog harbour, rain forest; tree; *Nodhe*; (31) 24. i. 34.

DRACONTOMELON VITIENSE Engl.—Hog harbour, rain forest; buttressed tree, with edible fruit; *Nadhpōl*; (324) 2. ii. 34; buttressed tree, green edible berries; (310) 1. ii. 34.

LEGUMINOSAE.

TEPHROSIA PURPUREA Pers.—Hog harbour, rain forest; *Lonenes*; (234) 24. i. 34.

HANSLIA ADHAERENS Schindl.—Hog harbour, rain forest ; pink flowers ; *Nwepraprur* ; (49) 20. xi. 33 ; shrub, leaves deciduous, spike of white papilio-naceous flowers, fruit a lomentum which adheres to the clothes ; (55) 22. xi. 33.

DESMODIUM ADSCENDENS Sw.—Hog harbour, clearings ; *Nwiturakara* ; (49 a) 4. i. 34.

D. UMBELLATUM DC.—Sana, Gaua Is. ; shrub, 15 ft., small white flowers ; *Quiquier* ; (339).

ENTADA GIGAS Fawcett & Rendle (*E. scandens* Benth.)—(271) fruit.

ERYTHRINA INDICA Linn.—Hog harbour, 350 ft., rain forest ; *Ndruru*. This is the tree whose flowering gives the signal for the planting of yams ; 13. xi. 33.

STRONGYLODON LUCIDUS Seem.—Without locality or number.

ABRUS PRECATORIUS Linn.—Hog harbour ; purple flowers ; (246) 24. i. 34.

PUERARIA NEO-CALEDONICA Harms.—Mt. Tabwemasana, 4000 ft., in cane grass, not very common ; a climber, purple flowers ; *Wasia* ; (18) 29. x. 33.

P. THUNBERGIANA Benth.—Hog harbour, rain forest ; climber ; *Nueha* ; (288) 27. i. 34.

CANAVALIA ENSIFORMIS DC.—Hog harbour, rain forest ; climber, pink flowers ; *Nwoivatnedh* ; (39) 20. xi. 33.

C. OBTUSIFOLIA Linn.—Hog harbour, 250 ft., among gardens ; (172) 8. i. 34.

PTEROCARPUS INDICUS Willd.—Hog harbour, rain forest ; *Nula* ; (276) 16. i. 34.

DERRIS TRIFOLIATA Lour. (*D. uliginosa* Benth.)—Hog harbour, rain forest ; creeper ; *Nwoiedh* ; (175) 4. xii. 33 : climber, pink flowers ; *Nuedhu* ; (242) 24. i. 34 : (282) 27. i. 34.

INOCARPUS EDULIS Forst.—Hog harbour, rain forest ; tree, 10 ft., dull leaves, spikes of small flowers ; *Némáp* ; (265) 25. i. 34 : tree, edible fruit ; *Némáp* ; (271) 26. xi. 33.

CASTANOSPERMUM AUSTRALE A. Cunn. & Fraser.—Hog harbour, rain forest ; *Nás* ; (5) 6. xi. 33.

CAESALPINIA BONDUC Roxb.—Hog harbour, rain forest ; climber ; *Nuak-serser* ; (217, 217 a) 24. i. 34.

C. NUGA Ait.—Hog harbour, rain forest ; climber ; *Wesatiodeh* ; (222) 24. i. 34.

CASSIA OCCIDENTALIS Linn.—Hog harbour, cleared field ; yellow flowers ; *Nédrabohboh* ; (62) 25. xi. 33.

AFZELIA BIJUGA A. Gray.—Hog harbour, rain forest ; tree, hard wood used for building houses, small oval glaucous leaves ; *Notor* ; (228) 24. i. 34 ; tree, enormous lomentum ; (313) 1. ii. 34.

ACACIA SPIRORBIS Labill.—Hog harbour, rain forest ; tree, yellow flowers ; (297) 29. i. 34.

RHIZOPHORACEAE.

RHIZOPHORA CONJUGATA Linn.—Gaua Is., mangrove ; (302) i. 34.

COMBRETACEAE.

TERMINALIA CATAPPA Linn.—Hog harbour ; (105). Tree.

MYRTACEAE.

EUGENIA RICHII A. Gray.—Hog harbour, rain forest ; *Né* ; (104) 19. xii. 33.

PSIDIUM GUAJAVA Linn.—Hog harbour, rain forest ; shrub, thick dull leaves, veins protruding beneath, 2 inches, edible fruit, with pink flesh ; *Ne guap* ; (331) 2. ii. 34.

LECYTHIDACEAE.

BARRINGTONIA ASIATICA Kurz (*B. speciosa* Forst.).—Hog harbour, sea-shore ; *Nuap* ; (231) 24. i. 34.

MELASTOMACEAE.

MEDINILLA sp. aff. **HETEROMORPHOPHYLLA** Guillaum.—Gaua Is. ; pale pink outside, dark pink inside ; (346) i. 34.

MELASTOMA DENTICULATUM Labill.—Mt. Tabwemasana, 4,000 ft., open grassland ; shrub, about 1 ft. high, white flowers ; (35) 29. x. 33.

CARICACEAE.

CARICA PAPAYA Linn., var.—Hog harbour, rain forest ; (293) 27. i. 34, ♂ ; clearing ; flowers and stem of inflorescence red, not indigenous ; (206) 21. i. 34 : without locality ; (251).

CUCURBITACEAE.

TRICHOSANTHES ?—Hog harbour, rain forest ; climber, large orange-coloured berry, black seeds, the fruit eaten ; *Néwarsan* ; (77) 23. i. 34.

TRICHOSANTHES ?—Hog harbour, rain forest ; climber, fruit a red trilocular berry with red flesh, 2–3 in. long, rounded ; *Nwarüm* ; (86) 23. i. 34.

MELOTHRIA BAUERIANA F. Muell. ?—Hog harbour, rain forest ; *Nuanea* ; (296) 27. i. 34, ♂ : (315) 1. ii. 34, ♀. Identical with plants collected at Ambrym by M. and Mme de la Rue (see *Bull. Mus. sér. 2, IX*, p. 288, 1937).

LUFFA probably **CYLINDRICA** Nutt. var. **INSULARUM** Cogn.—Sara, garden ; *Nuepatuiara* ; (129) 27. xii. 33.

BEGONIACEAE.

BEGONIA sp.—Mt. Tabwemasana, 3,000–5,000 ft., mossy forest, common, 3 ft. high, white flowers ; (34) 10. ii. 33.

This specimen, bearing only ♂ flowers, seems different from the one (without flowers) collected at Pentecost Island by Aubert de la Rue. A *Begonia* was enumerated (without authenticating specimen) by Kajewski as on Vanua Lava island.

ARALIACEAE.

DELARBREA COLLINA Vieill.—Hog harbour, rain forest ; *Mcintoshalkara* ; (295) 29. i. 34 : *Névarkrab* ; (72) 28. ii. 34.

MERYTA sp.—Hog harbour, rain forest ; tree, petioles enlarged for about 1 inch where they join stem ; *Nvalval* ; 90 ft. ; (12) 30. x. 33 : (24) 11. xi. 33.

TIEGHEMOPanax FRUTICOSUS R. Viguer.—Tungwi, garden, yellow leaves ; *Nülüh* ; (156) 29. xii. 33.

T. NUSEDHUL Guillaum., sp. nov.—*Glaberrima*, . . . *Foliola* ovato-elongata (usque ad 27 cm. \times 8 cm.), basi valde asymmetrica cordata, apice acute acuminata, integra, sat crassa, petiolulo robusto 1 cm. longo. *Inflorescentiae* paniculatim capitatae, ramis usque ad 15 cm. longis, bracteis ovato-triangularibus acute acuminatis 5–7 mm. longis, capituli pedunculo 2–4 mm. longo. *Flores* circa 10-ni, sessiles, 2 mm. longi, basi bracteolati. *Calyx* truncatus, margine undulato. *Petala* . . . *Stamina* . . . *Discus* planus. *Ovarium* 2-loculare, stylis 2 1 mm. longis usque ad medium liberis longitudinaliter sulcatis.

Hog harbour, rain forest ; *Nüsedhul* ; (13 a) 24. i. 34 : (71 a) 28. xi. 33.

T. EXCELSA Guillaum., sp. nov.—30 m. alta, *glaberrima*, . . . *Foliola* ovato-falciformia (usque ad 24 cm. \times 10 cm.), basi cordato-auriculata, apice acuta, tenuia, nervis 10–18-jugis, petiolulo 1·5 cm. longo. *Inflorescentiae* paniculatim umbellatae, ramis usque ad 25 cm. longis, bracteis triangularibus crassis 1 cm. longis, umbellulae pedunculo circa 5 mm. longo, floribus 6–10-nis 30 mm. longis, pedicello 1 mm. longo apice articulato. *Calyx* truncatus, minute acute 5-dentatus. *Petala* 5, lanceolata, intus medio carinata apiceque filamentose appendiculata. *Stamina* 5, antheris ovatis, filamentis antheris brevioribus. *Styli* 2, brevissimi, connati.

Hog harbour, rain forest ; *Nüsedhül* ; (13) 30. x. 33.

POLYSCIAS PINNATA Forst.—Hog harbour, rain forest ; *Nëwesi* ; (64) 27. xi. 33 : shrub, inflorescence about 2 ft. long ; *Nüesi* ; (261), 25. i. 34.

SCHEFFLERA NEO-EBUDICA Guillaum. ?—Between Ladhogh and Turworsoksok, rain forest ; *Narkü* ; (138) 28. xii. 33.

BOERLAGIODENDRON ORIENTALE Guillaum., sp. nov.—*Folia* 40 cm. longa, petiolo 15 cm. longo basi extra fimbriato cristato, lamina glaberrima basi rotundata usque ad medium 3-secta, segmentis ovatis apice obtusis margine grosse serratis. *Umbellae* 8–11 cm. longae, multiflorae, alabastris sessilibus 1 cm. pedicellatis 6 cm. longis. *Ovarium* turbinatum, ore truncatum. *Corolla* globosa. *Stamina* 4, filamentis antheram aquantibus. *Ovarium* 5-loculare.

Hog harbour, rain forest ; *Varakü* ; (258) 25. i. 34.

Inflorescence a large compound umbel, even, 1 ft. across, red fruits. A species of the *Pedicellata* group, near *B. novo-guineense*. No species previously known eastward of New Guinea.

RUBIACEAE.

BIKKIA PANCHERI Guillaum.—Hog harbour, near the sea ; shrub ; *Newav* ; (59) 24. xi. 33. Unknown, till now, in the neighbourhood of New Caledonia.

CHOMELIA ?—Hog harbour, rain forest ; white leaves ; *Lasker* ; (255) 25. i. 34.

GARDENIA sp.—Hog harbour, rain forest ; large glaucous leaves, dark green, white-veined ; *Bior* ; (216) 24. i. 34.

PAVETTA INDICA Linn.—Hog harbour, rain forest ; white flowers ; (239) 24. i. 34 : shrub, white flowers, green stamens ; *Posolok* ; (260) 24. i. 34.

CALYCODENDRON MILNEI A. C. Smith.—Between Sara and La'dhogh, rain forest ; shrub ; (115) 27. xii. 13 : 90 ft., rain forest ; (8 a) 11. xi. 33.

MORINDA CITRIFOLIA Linn.—Hog harbour, rain forest ; tree ; (298) 29. i. 34.

PSYCHOTRIA ANEITYENSIS Guillaum.—Hog harbour, 100 ft., rain forest ; one of the very commonest bushes ; *Kerkerarodh* ; (6) 27. x. 33.

P. ANEITYENSIS ?—Hog harbour, 90 ft., rain forest ; *Yal yal rara* ; (29) 11. xi. 33.

PSYCHOTRIA sp.—Hog harbour at 90 ft., rain forest ; (27) 11. xi. 33 : at 200 ft. in rain forest ; a bush with white flowers, red and green berries ; *Kerkerarodh* ; (8) 17. x. 33 ; mixed with no. 66—*Ervatamia orientalis*.

GEOPHILA HERBACEA Kuntze.—Hog harbour, 100 ft., rain forest ; small herb with white flowers and red berries ; *Nidhvura* ; (7) 18. x. 33.

OPHIORRHIZA cf. **HARRISIANA** Heyne.—Hog harbour, rain forest, near sea ; (88) 9. xii. 33.

COMPOSITAE.

VERNONIA CINEREA Less.—Hog harbour, garden ; (198) 14. i. 34 : Shark bay clearing ; *Nesepi* ; (149) 29. xii. 33 ; Nopu, 2000 ft., grassy hills, grows 2 ft. high ; *Palise taboa taboa* ; (23) 10. xi. 33.

ADENOSTEMMA VISCOMUM Forst.—Hog harbour, rain forest ; white flowers ; *Netenvu* ; (95) 10. xii. 33.

ERIGERON BONARIENSIS Linn.—Tungwi, garden ; *Wii hogh tovkara* ; (90) 10. xii. 33 : between Shark bay and Hog harbour, clearing in rain forest ; (165) 30. xii. 33.

CONYZA VISCIDULA Wall.—Mt. Tabwemasana, 4,000 ft., grass land ; small plant, 2 ft. high, pale mauve flowers ; (31) 29. x. 33.

AGERATUM CONYZOIDES Linn.—Mt. Tabwemasana, 4,000 ft., grass land ; small white flowers, very common ; (19) 29. x. 33.

BLUMEA CHINENSIS DC.—Hog harbour ; herb, yellow flowers ; (351) 7. ii. 34.

SIEGESBECKIA ORIENTALIS Linn.—Mt. Tabwemasana, 4,000 ft., open grass land, 1 ft. high ; small yellow flowers, rare ; (30) 29. x. 33.

ECLIPTA ERECTA Linn.—Gaua Is., along water's edge ; like a Michaelmas daisy ; (347) i. 34.

WEDELIA ARISTATA Less. (*W. biflora* DC.).—Mt. Linisupe, 3,000 ft., steep grass slope, about 2 ft. high ; bright yellow flowers ; (28) 1. xi. 33 : Hog harbour, near the sea ; yellow flowers ; *Nesenu* ; (56) 24. xi. 33.

GOODENOVIACEAE.

SCAEVOLA NEO-EBUDICA Guillaum.—Mt. Tabwemasana, 4,000 ft., edge of forest and grass land, bush about 12–15 ft. high ; *Papisso* ; (21) 29. x. 33.

CAMPANULACEAE.

LOBELIA sp. cf. *QUADRANGULARIS* R. Br.—Mt. Tabwemasana, 4,000 ft., open grass land; small plant, white flowers with dark purple stripes; (26) 29. x. 33*.

MYRSINACEAE.

MAESA AMBRYMENSIS Guillaum.—Mt. Tabwemasana, 5,000 ft., mossy forest; shrub, 3 ft., minute white flowers, white berries; (32) 30. x. 33.

M. AUBERTII Guillaum.—Hog harbour, rain forest; shrub; *Nudherak*; (333) 2. ii. 34.

SAPOTACEAE.

MIMUSOPS PARVIFLORA R. Br.—Hog harbour, rain forest; *Ner*; (233) 24. i. 34: wood said to be very hard; (200) 19. i. 34.

SAPOTACEA, perhaps *LUCUMA*.—Without locality; large oval edible fruit; *Nunget*; (232).

APOCYNACEAE.

ALYXIA cf. *SCANDENS* Room. & Schult.—Tungwi, rain forest; (154) 29. xii. 33: between Lowerie and Ladhogh, rain forest; shrub; *Yalyal*; (137) 27. xii. 33.

KOPSIA FRUTICOSA A. DC. ?—Hog harbour, rain forest; white flower, purple centre; (274) 26. i. 34.

ERVATAMIA ORIENTALIS Turrill.—Hog harbour, rain forest; white flowers; shrub, lanceolate leaves, white hypocrateriform corolla, fruit red when ripe; *Népangpang*; (66) 27. xi. 33; mixed with *Psychotria* sp.

PARSONSIA INAE † Guillaum., sp. nov.—Scandens. *Folia* opposita, late ovata (usque ad 11 cm. × 8 cm.), apice breviter acute acuminate, basi rotundata, nervis 8–5-jugis, petiolo 2·5–3 cm. longo. *Inflorescentia* terminalis, multiflora, ad 7 cm. longa, pedunculo 1·5 cm. longo, ramis circa 1 cm. longis, bracteis minimis anguste triangularibus, pedicellis 5 mm. longis basi minute puberulis. *Calycis* lobi triangulares, 2 mm. longi, margine ciliolati, squamis lanceolatis dimidio breviores. *Corolla* 8 mm. longa, lobis linearibus tubo longioribus, tubo cylindrico. *Stamina* corollae lobis fere aequilonga, antheris quarta infima parte fissa, filamentis tortis vix breviora, squamis hypogynis lanceolatis. *Ovarium* squamis vix longius, glabrum. *Folliculus* 11 cm. longus, 7 mm. diam.

Hog harbour, rain forest; climber, greenish flowers, yellow stamens, fruit containing seeds with pappus; *Noevatri*; (205) 21. i. 34.

Near *P. affinis* Baill. of New Caledonia and *P. Cummingiana* A. DC. of the Philippine Islands.

PARSONSIA?—Hog harbour, rain forest; climber; *Nuenuk*; (327) 2. ii. 34.

APOCYNACEA! cf. *CARRUTHERSIA*.—Hog harbour, rain forest; climber, with opposite laurel-like leaves, opposite peduncles joining round main stem, 5 in., fruit contains seeds with pappus; *Nuenuk*; (335) 2. ii. 34.

* Found also at Ambrym, at the top of the crater of Mt. Marum, 1,100 m. Plant creeping on the soil (Aubert de la Rue, 2nd voyage, 9. x. 36).

† After Miss Ina Baker.

ASCLEPIADACEAE.

HOYA NEO-EBUDICA Guillaum.—Gaua Is.; climber, whitish mauve flowers; (342) i. 34.

SECAMONE ATTENUATA Dene.—Hog harbour, rain forest; shrub, flowers yellow; *Yalyalkara*; (238) 24. i. 34.

TYLOPHORA ACUTIPETALA Guillaum., sp. nov.—*Rami* graciles, flexuosi, laxe foliati, glaberrimi. *Folia* ovata (usque ad 7 cm. \times 4 cm.), tenuia, basi sub-emarginata, apice acuta apiculataque, nervis 6–7-jugis, petiolo gracili circa 2 cm. longo. *Inflorescentiae* axillares, usque ad 10 cm. longae, 2–3 gradatim cymosae, pedunculo infimo circa 5 cm. longo, secundo tertioque 4–3 cm. longo, pedicello capillari 1 cm. longo. *Calycis* segmenta ovata, 1 cm. longa, tertia infima parte coalita, apice rotundata, margine ciliolulata. *Corollae* segmenta lanceolata, apice acuta, basi tantum $\frac{1}{2}$ connata, 7-nervia, coronae squamis carnosus nigrisque rhomboideis antherarum medium attingentibus. *Antherae* parallelipipedes, apice truncatae, appendice hyalino coronatae, pollinibus ovatis, translatoribus brevibus, retinaculo rhomboideo. *Fructus* globosus.

Hog harbour; *Nwoiwalti*; (108) 20. xii. 33.

Near *T. Brackenridgei* A. Gray, but inflorescences 5–6 times longer than the petiole and with 2–3 tapering flowers.

LOGANIACEAE.

GENIOSTOMA RUPESTRIS Forst.—Mt. Tabwemasana, 4,000 ft., open grassland; small shrub, 3 ft. white flowers; (129) 29. x. 33.

BORAGINACEAE.

CORDIA MYXA Linn.—Cymose inflorescence of small white flowers; *Napudh*; (207).

C. SPRENGELII DC.—Hog harbour, rain forest; tree; bark used for making baskets; *Nepāken*; (247) 1. ii. 34.

C. SUBCORDATA Lam.—Hog harbour, Blue water, rain forest; *Nepāken*; (103) 18. xii. 33.

CONVOLVULACEAE.

IPOMOEA BONA-NOX Linn.—Hog harbour, rain forest; *Nūehu*; (57 a) xii. 33: climber; (314) 1. ii. 34: deserted garden, white flower; (57) 24. ii. 33.

I. DENTICULATA Choisy.—Hog harbour, garden (native); *Nwisiknaghakara*; (303) 31. i. 34.

I. DENTICULATA Choisy?—Hog harbour, in a clearing; pink flower; *Nwoikdhaw*; (110) 2. xii. 33.

I. PELTATA Choisy.—Hog harbour, rain forest; deserted gardens become covered over with this creeper; *Nweli*; (308) 1. ii. 34.

I. TURPETHUM R. Br.?—Hog harbour, rain forest; climber; *Nuerāp*; (326) 2. xi. 33.

SOLANACEAE.

SOLANUM FEROX Linn.—Ladhogh, gardens ; *Sukakeri* ; (124) 27. xii. 33.
S. NIGRUM Linn.—Hog harbour, rain forest ; *Nepor* ; (50) 20. xi. 33.
S. TETRANDRUM R. Br.—Hog harbour, in the grass ; white petals, yellow stamens, green berries ; (58) 24. xi. 33.
S. VIRIDE R. Br.—Hog harbour, rain forest ; white flower, red berries ; (285) 27. i. 34.
S. sp.—Hog harbour, gardens ; white flower, yellow stamens, fruit edible ; *Nesporlporl* ; (349) 7. ii. 34.
CAPSICUM MINIMUM Roxb.—Hog harbour, rain forest, gardens ; “ wild Chilli ” ; *Bima* ; (41) 20. xi. 33.
LYCOPERSICUM ESCULENTUM Mill.—Hog harbour, rain forest ; “ wild Tomato ” ; *Teonanterasal* ; (51) 20. xi. 33.

SCROPHULARIACEAE.

LINDERNIA CRUSTACEA F. Muell.—Mt. Tabwomasana, 4,000 ft., open grass-land, fairly common ; very small, compact growth, mauve flowers ; (20) 29. x. 33.

VERBENACEAE.

STACHYTARPHETA INDICA Vahl.—Hog harbour, covers the ground in the Coconut plantations ; an imported curse ; (211) 23. i. 34.
PREMNA INTEGRIFOLIA Linn.—Hog harbour ; *Nëvernvern* ; (81) 6. xii. 33.
VITEX TRIFOLIA Linn.—Between Shark bay and Hog harbour, garden ; shrub ; (170) 30. xii. 33.
CLERODENDRON FALLAX Lindl.—Hog harbour, gardens ; (112) 12. i. 34.
C. INERME R. Br.—Between Shark bay and Hog harbour ; (168) 30. xii. 33 : Hog harbour, strand ; white flowers, purple stamens ; *Naviaradhé* ; (226) 24. i. 34.

LABIATAE.

OCIMUM CANUM Sims.—Hog harbour, gardens ; *Neruk* ; (323) 1. ii. 34 ; Gaua, native villages ; white flowers ; *Maban* ; (340) i. 34.
COLEUS SCUTELLARIOIDES Benth.—Hog harbour ; *Naporda* ; 10. i. 34.
SALVIA SPLENDENS Ker-Gawl.—Tungwi, garden ; *Nepor* ; (155) 29. xii. 33. [Same vernacular name as *Solanum nigrum*.]

NYCTAGINACEAE.

CALPIDIA EXCELSA Heimerl.—Hog harbour, rain forest ; dirty white flowers ; *Nerunge* ; (336) 3. ii. 34 : tree ; *Nepangi* ; (330) 2. ii. 34.

AMARANTHACEAE.

CYATHULA PROSTRATA Bl.—Hog harbour, rain forest ; purplish stems, green flowers, pink hairs on bracts ; (90) 10. xii. 33.
AMARANTHUS BLITUM Linn.—Hog harbour, fields ; (176) 13. i. 34.

A. MELANCHOLICUS Moq. var **OBOVATA** Moq.—Gaua Is. ; 5 ft. high, brilliant cerise leaves ; *Theg* ; (341) i. 34. Var. **LINEARIS** Guillaum.—Hog harbour, gardens ; leaves brilliant magenta ; *Nèvèv* ; (321) i. ii. 34.

GOMPHRENA GLOBOSA Linn.—Hog harbour, gardens ; worn in the hair sometimes ; *Nèsern* ; (312) i. ii. 34. Var. **PURPUREA** (312 a).

IRESINE HERBSTII Hook. var. **AUREO-RETICULATA**.—Mt. Tabwemasana, 4,000 ft., mossy forest ; grows about 4 ft. high where forest clears a little ; (25) 3. xi. 33.

TELANTHERA MARITIMA Moq.—Hog harbour, field ; (177) 13. i. 34.

T. POLYGONOIDES Moq.—Hog harbour, garden ; can be eaten as cabbage ; (180) 13. i. 34.

PHYTOLACCACEAE.

MONOCOCCUS ECHINOPHORUS F. Muell. ?—Ladharo island ; antidote to poison ; (163) 29. xii. 34.

POLYGONACEAE.

POLYGONUM SUBSESSILE R. Br.—Gaua Is., in warm part of lake where 3 ft. deep ; 2 ft. above water, small white flowers ; (345) i. 34.

ARISTOLOCHIACEAE.

ARISTOLOCHIA RUIZIANA Duch.—Hog harbour, Missionary's Garden ; Pitcher plant ; (355) 8. ii. 34.

PIPERACEAE.

PIPER LATIFOLIUM Linn. f. ?—Hog harbour, rain forest ; *Nèkudh* ; (61) 24. ii. 33.

P. METHYSTICUM Forst. f.—Hog harbour, rain forest, 90 ft. ; *Nèvülko* ; (15) 2. xi. 33.

P. aff. BETLE Linn.—Hog harbour, rain forest, 90 ft. ; climbing Kava ; *Nèvulkohā* ; (35) 16. xi. 33.

P. aff. EXCELSUM Forst.—Between Gaua and Ladhogh, rain forest ; *Nèvulkavo* ; (122) 27. xii. 33.

PEPEROMIA LEPTOSTACHYOIDES C. DC.—Hog harbour, rain forest, 250 ft. ; grows out of a coral cliff ; (76) 4. xii. 33.

MYRISTICACEAE.

MYRISTICA sp.—Hog-harbour, rain forest, 90 ft. ; *Nèklugh* ; (33) 16. xi. 33.

MONIMIACEAE.

HEDYCARIA sp.—Hog harbour, rain forest ; shrub, green fruit borne on button-shaped thalamus, 6 in. leaves ; *Warwariok* ; (264) 25. i. 34.

HERNANDIACEAE.

HERNANDIA CORDIGERA Vieill. or **PELTATA** Meissn.—Hog harbour, strand : *Dhürdhür* ; (232) 24. i. 34.

LORANTHACEAE.

ELYTHRANTHE BANKSIANA Guillaum.—Hog harbour, rain forest; parasite on other trees; yellow flowers; *Nütler*; (230) 24. i. 34.

EUPHORBIACEAE.

PHYLLANTHUS sp.—Hog harbour, rain forest; shrub, green flowers; *Dran*; (42) 20. xi. 33.

P. sp.—Hog harbour; red berries, white flowers; *Nèdran*; (249) 25. i. 34.

GLOCHIDION RAMIFLORUM Forst.—Hog harbour, rain forest, 300 ft.; very hard and durable timber used in building native houses; said not to occur in the islands of Efate and Malekula; *Nevaghur*; (74 b) 7. x. 33: (74 a) 28. xi. 33: (74) 18. xii. 33.

JATROPHA CURCAS Linn.—Hog harbour, clearings; not indigenous; *Nedrulda*; (203) 21. i. 34.

ALEURITES MOLUCCANA Willd.—Hog harbour, rain forest; large tree; the seed is chewed and spat into the spathe of a Coconut palm, which is then twisted until oil runs out which is used to make the hair soft, and is also rubbed into the skin; *Nèpa*; (221) 24. i. 34.

CODIAEUM VARIEGATUM Müll.-Arg.—Hog harbour, rain forest; shrub; (78) 61. i. 34: *Nrakarakara*; (78 a) 24. i. 34: (54) 22. xi. 33: (87) 9. xii. 33: gardens; (113) 12. i. 34: Shark bay, 200 ft., clearings; *Lakalakala*; (148) 29. i. 34.

FONTAINEA PANCHERI Heck.—Hog harbour, rain forest; large tree, hard wood used for building houses, glaucous lanceolate leaves, apple-like fruit; *Namsun*; (244) 24. i. 34.

MANIHOT UTILISSIMA Müll.-Arg.—Hog harbour, gardens; the root is eaten; Manioc; (268) 25. i. 34.

CLAOXYLON BICILIATUM Guillaum., sp. nov.—*Arbor*; ramuli novelli parce tomentosi, mox glabrescentes. *Petiolus* 2·5–4·5 cm. longus, glabrescens, apice subulato 2-glandulosus: lamina 10–13 cm. longa, 4–7 cm. lata, ovata, basi cuneata, apice acuminata, margine undulato-serrata, laevis, membranacea, adulta glabra; venae subtus tenuer prominentes. *Flores* dioici. *Racemi* ♂ 3–5 cm. longi, basi breviter nudi: rachis sat gracilis, tenuiter pubescens: bracteae circa 5-florae: flores fasciculati: pedicelli tenuiter pubescentes, circa 2 mm. longi: alabastrum globosum, per anthesin 4-fidum. *Tepala* spathulata, 2 mm. longa, apice obtusa, extra sparse pubescentia. *Stamina* circa 30, filamenta filiformia, glabra, antheris 2–3-plo longiora. *Glandulae* juxtastaminales clavatae, apice ciliis 2 albis munitae.

Hog harbour, rain forest; *Nevaogh*; (25) 23. i. 34.

Ad *C. insularum* Müll.-Arg. referens; sed petioli glandulae subulatae, inflorescentiae ♂ breviores, glandulae juxtastaminales apice tantum 2-ciliatae.

ACALYPHA GRANDIS Müll.-Arg.—Hog harbour, gardens; green leaves and flowers; (194) 14. i. 34: between Shark bay and Hog harbour, rain forest; (164) 30. xii. 33.

A. HISPIDA Burm. f.—Hog harbour, garden ; red flowers, green leaves ; (191) 14. i. 34.

Var. ALBA Hort.—Hog harbour, garden ; white flowers, green leaves ; (192) 14. i. 34.

A. WILKESIANA Müll.-Arg.—Hog harbour, garden ; believed not to grow in bush ; (179) 13. i. 34 : cuttings or seedlings of 179, with red leaves ; (196) 14. i. 34.

A. WILKESIANA Müll.-Arg. form. CIRCINNATA Müll.-Arg. subform. foliis discoideis flabelliformibus rubris. Hog harbour ; gardens, cuttings or seedlings of 179 ; (193) 14. i. 34. Subforma foliis reniformibus viridibus rubromaculatis. Hog harbour, garden ; cutting or seedlings of 179 ; (190) 14. i. 34.

A. sp. cf. FORSTERIANA Müll.-Arg.—Hog harbour, rain forest ; Narev ; (53) 22. xii. 33 : Naro ; (266) 25. i. 34.

CLEIDION JAVANICUM Bl.—Hog harbour, rain forest ; (338) 7. ii. 34.

EXCOECARIA AGALLOCHA Linn.—Hog harbour, rain forest ; large tree, milky sap ; Nétotnevakara ; (229) 24. i. 34.

MACARANGA DIOICA Müll.-Arg.—Rain forest ; tree ; Netekun ; (70) 28. xi. 33.

M. sp. aff. TANARIUS Müll.-Arg.—Hog harbour, rain forest ; Nétekum ; (320) 2. i. 34.

M. sp.—Hog harbour, rain forest ; tree ; *Megapodius layardi* makes its nest in the dead stump ; Nugamara ; (272) 26. i. 34.

M. sp.—Hog harbour, rain forest ; small tree ; Tekunkar ; (224) 25. i. 34.

HOMALANTHUS EBRACTEATUS Guillaum. !—Mt. Tabwemasana, 5,000 ft., mossy forest ; small tree, about 6 ft. ; (24) 30. x. 33.

H. NUTANS Pax.—Hog harbour ; Nésal ; (84) 6. xii. 33.

MORACEAE.

FICUS COPIOSEA Steud.—Hog harbour ; tree, lanceolate leaves ; Nédhelagh ; (67) 27. xi. 33.

F. MOSELEYANA King.—Hog harbour, rain forest ; white-veined leaves, fig large, 10 in. ; Worworker ; (223) 24. i. 34.

F. SEPTICA Burm. f.*.—Hog harbour, rain forest, 90 ft. ; flying foxes eat the fruits ; Worawora ; (26) 11. ii. 33.

F. STENOCARPA F. Muell. (*F. Proteus* Burk.).—Hog harbour, rain forest ; Adhaladhabara ; (83) 6. xii. 33.

F. TRICHONEURA Summerh.—Hog harbour, rain forest ; small tree, dull green leaves ; Nélim ; (263) 25. i. 34.

ANTIARIS BENNETTII Seem.*.—Hog harbour, rain forest ; tree, red fruit ; Nesu ; (127 a) 23. i. 34 : between Lowerie and Ladhogh, rain forest ; red fruit about 1½ in. ; Nesu ; (127) 27. xii. 33.

* Determined by V. S. Summerhayes.

URTICACEAE.

FLEURYA INTERRUPTA Gaudich.—Between Turworsoksok and Shark bay, rain forest ; a nettle, the natives say it stings ; *Simlagodh* ; (146) 29. xii. 33.

LAPORTEA CRENULATA Gaudich.—Hog harbour, rain forest, 90 ft. ; stings ; *Nogoladh* ; (30) 14. ii. 33 : Morsal, rain forest, very common ; young leaves sting badly, causing a sleepless night, with pain lasting for days ; *Nogoladh* ; (145) 29. xii. 33.

LAPORTEA ?—Hog harbour, rain forest ; shrub, pink stalks to inflorescence and pink calyx, white flowers ; *Ladgar* ; (262) 25. i. 34.

PROCRIS cf. PEDUNCULATA Wedd.—Hog harbour, rain forest ; 90 ft., climber ; *Lo* ; (36) 16. ii. 33 : *Nasukonru* ; 30. x. 33.

P. sp.—Between Morsal and Shark bay, rain forest ; (151) 28. xii. 33.

CYPHOLOPHUS MOLUCCANUS Miq. (*C. macrocephalus* Wedd.).—Between Sara and Ladhogh, rain forest ; *Pangsurl* ; (121) 27. xii. 33.

PELLIONIA ELATOSTEMOIDES Gaudich, ♂.—Hog harbour, rain forest ; climbs, rooting on trees, fleshy stem, white flowers ; *Nwarmallil* ; (37) 20. ii. 33.

PIPTURUS ARGENTEUS Wedd. var. *LANOSUS* Skottsb.—Hog harbour ; *Nerui* ; (237) 24. i. 34.

PSEUDOPIPTURUS REPANDUS Skottsb.—Hog harbour, rain forest ; (38) 20. xi. 33 : *Néweroli* ; (332) 2. ii. 34.

MAOUTIA AUSTRALIS Wedd.—Mt. Tabwemasana, mossy forest, 5000 ft. ; shrub about 4 ft. high ; minute white flowers on red stems ; (17) 30. x. 33.

LEUCOSYKE CAPITELLATA Wedd.—Between Sara and Ladhogh, rain forest ; *Lünka* ; (133) 27. xii. 33.

CASUARINACEAE.

CASUARINA EQUISETIFOLIA Linn.—Hog harbour, strand ; *Némās* ; (287) 27. i. 34.

ORCHIDACEAE*.

LIPARIS CONDYLOBULBON Reichb. f.—Between Ladhogh and Turworsoksok, rain forest ; *Néswarol* ; (142) 28. xii. 33.

L. MATAASENSIS J. J. Sm. ?—Mt. Tabwemasana, 5000 ft., mossy forest ; grows on mossy ground, about 1 ft. high, dark purple flower and stem ; (15) 2. xi. 33.

DENDROBIUM MACRANTHUM A. Rich.—Variety with very narrow petals. Hog harbour, sea-level, on tree by sea shore ; flowers white with mauve in labellum ; 1. i. 34.

PEDILOCHILUS sp.—Mt. Tabwemasana, 6000 ft., on mossy branches of trees ; small creeping Orchid, purple brown flower, very rare (Guillaumin, 1935) ; 30. x. 33 : mossy forest, 6000 ft., mossy branches of trees ; pale yellow flower, common (Rolfe, 1909) ; 30. x. 33. The genus is allied to *Bulbophyllum*, and is almost entirely confined to New Guinea.

MALAXIS NEO-EBUDICA Ames.—Between Shark bay and Hog harbour, rain forest ; *Hōphōp* ; (169) 30. xii. 33.

* Determined by Ch. Schweinfurth.

SPATHOGLOTTIS PETRI Reichb. f.—Mt. Tabwemasana, 4000 ft., in low grass-land, very common ; all shades from pale to dark mauve ; (6) 29. x. 33.

PHAIUS sp. aff. **TANCARVILLEAE** (Banks) Bl.—Tatarii district, 3000 ft. ; grows in short cane grass on hill side ; about 3 ft. high, 2 orange-brown sepals, 2 red-brown petals, labellum yellow, mauve mouth ; (7) 1. ii. 33.

GLOMERA MACDONALDII J. J. Sm.—Mt. Tabwemasana, 6,000 ft., on mossy tree ; hangs in branches, common ; about 1-2 ft. long, white flowers ; (1) 30. x. 33.

COELOGYNE LAMELLATA Rolfe.—Mt. Tabwemasana, 6,000 ft., mossy forest, hangs in branches, common ; pale green fleshy sepals, petals brown and yellow striped, leaves a foot long ; (11) 30. x. 33.

SPIRANTHES SINENSIS (Pers.) Ames.—Mt. Tabwemasana, 3,000 ft., open grassland ; small mauve flowers ; (16) 4. xi. 33.

VRYDAGZYNEA CHEESEMANII Ames.—Hog harbour ; white flowers ; (136) i. 34 : between Morsal and Shark bay, rain forest ; (162) 29. xii. 33.

PRISTIGLOTTIS FIMBRIATA (J. J. Sm.) Cretz. & J. J. Sm. (*Cystopus fimbriatus* J. J. Sm.).—Mt. Linisupe, 5,000 ft., mossy forest ; 1 foot high, white fleshy flower ; (5) 1. i. 34.

HABENARIA STENODON Reichb. f.—Hog harbour, rain forest ; white flowers, (173) 8. i. 34 : between Sara and Ladhogh, rain forest ; *Harohedh* ; (119) 27. xii. 33.

ZINGIBERACEAE.

GUILLAINIA NOVO-EBUDICA F. Muell. (*Alpinia Blumei* K. Schum., non D. Dietr.). Sara, rain forest ; red flowers ; (98) 13. xii. 33.

Forma **VARIEGATA**.—Hog harbour ; grows about 5 ft. high, leaves white and green, bracts whitish ; *Narpü* ; (243) 24. i. 34 *.

ZINGIBER ZERUMBET (Linn.) Rosc. ex Sm.—Hog harbour, rain forest ; *Narpü* ; (212) † 24. i. 34.

COSTUS SPECIOSUS (Koen.) Sm.—Hog harbour, rain forest ; leaves veined lengthwise, sheath surrounding stalk, flowers white, calyx red ; *Néreter* ; (214) 24. i. 34.

ALPINIA sp.—Between Ladhogh and Turworsoksok, rain forest ; white fruit ; *Nevās* ; (141) 28. xii. 33.

ALPINIA sp.—Hog harbour, rain forest ; slightly red berries, 1 in., white flesh, dark brown seeds ; *Novlün* ; (213) 24. i. 34.

ALPINIA ?—Hog harbour, garden ; white flowers ; (188) 14. i. 34.

ZINGIBERACEA.—Hog harbour, rain forest ; *Nervaswogh* ; (220) 24. i. 34.

CANNACEAE.

CANNA INDICA Linn.—Hog harbour, rain forest ; red trimerous flowers in spikes, purple stems and bracts ; *Nesort* ; (102 a) 18. xii. 33.

* Baker (in *sched.*) thinks it is the variegated form of the number 212 ; it is certainly the variegated form of the number 98 !

† Probably a confusion with the number 243.

MARANTACEAE.

CLINOZYNE DICHOTOMA (Roxb.) Salisb. (*Donax arundastrum* auct., non Lour.).—Hog harbour, rain forest ; leaves grow very large and are used for wrapping puddings while they are being cooked ; *Nelas* ; (269, 269 a) 25. i. 34.

DONAX CANNIFORMIS (Forst. f.) Rolfe (*Actoplanes canniformis* (Forst. f.) K. Schum.).—Hog harbour, rain forest ; white flowers ; *Nraiül* ; (91) 10. xii. 33 : (102).

MUSACEAE.

HELICONIA BIHAI Linn.—Hog harbour ; portion of leaf used for wrapping puddings for cooking in native ovens ; *Nusiare* ; (259) 25. i. 34.

LILIACEAE.

SMILAX cf. HERBACEA Linn.—Hog harbour, rain forest, 90 ft. ; climber ; *Welot* ; (34 a) 16. xi. 33.

S. VITIENSIS (Seem.) A. DC.—Hog harbour, rain forest ; trilocular berries, green to black ; *Në Welot* ; (34) 23. i. 34.

CORDYLINE TERMINALIS (Linn.) Kunth.—Hog harbour, rain forest ; single-stemmed shrub, with large, parallel-veined, unicostate leaves ; *Nekeli* ; (63) 17. xii. 33.

DIANELLA ENSIFOLIA (Linn.) Red.—Mt. Tabwemasana, open grassland, 4000 ft. ; *Olo-olo* ; (9) 29. x. 33.

COMMELINACEAE.

COMMELINA CYANEA R. Br.—Hog harbour, rain forest ; creeping growth, blue flower ; *Nehophop* ; (328) 2. ii. 34.

ZEBRINA PENDULA Schnizl.—Hog harbour, rain forest ; magenta flowers ; *Naiyetyet* ; (279) 26. i. 34.

POLLIA HORSTFIELDII C. B. Clarke, var. **MILNEI** C. B. Clarke.—Mt. Tabwemasana, in forest, 3000 ft. ; grows about 3–4 ft. high, white flowers ; *Mata-palipali* ; (8) 29. x. 33 : between Sara and Ladhogh, rain forest ; *Hōphōp* ; (136 b) 25. xii. 33.

COMMELINACEA ?—Between Ladbogh and Turworsoksok, rain forest ; *Nedhrokrok* ; (144) 28. xii. 33.

AMARYLLIDACEAE.

EURYCLES SYLVESTRIS Salisb.—Mt. Tabwemasana, mossy forest, 5000 ft. ; (13) 30. x. 33.

ZEPHYRANTHES ROSEA Lindl.—Hog harbour, field and garden ; pink flower ; (201) 20. i. 34.

CRINUM PEDUNCULATUM R. Br. ?—Hog harbour, garden belonging to the Government agent ; a strip of the leaf forms the dress of the native women ; (354) 8. ii. 34 : rain forest ; white flower ; *Komedhkara* ; (256) 25. i. 34.

DIOSCOREACEAE.

DIOSCOREA ESCULENTA (Lour.) Burk. (*D. fasciculata* Roxb.).—Hog harbour, gardens ; grown for the edible tubers, which is said to be similar to the ordinary yam but smaller ; *Halhalwotlam* ; (275) 26. i. 34.

PALMAE.

COELOCOCCUS WARBURGII Heim.—*Nētato*; (270).

Cf. *CYPHOPHOENIX*.—Hog harbour, rain forest; red fruit like a minute coconut; *Neorlal*; (318) 1. ii. 34: (361). „

PANDANACEAE.

PANDANUS COMINSII Hemsl.—Hog harbour, rain forest, 90 ft.; *Nēvor*; (21) 9. xi. 33.

FREYCINETIA TANNAENSIS Martelli.—Mt. Tabwemasana, mossy forest, 6000 ft.; grows in tufts and then creeping and climbing; (without number) 30. x. 33.

ARACEAE.

SCINDAPSUS sp. nov. ? aff. *PICTUS* Hassk.—Hog harbour, rain forest, 90 ft.; climbs by means of rootlets, leaves small as long as it grows along the ground, becoming larger as the stem grows up the trees; *Nasling*; (19) 9. xi. 33.

ALOCASIA ? or *COLOCASIA* ?—Hog harbour, rain forest; *Nuardh*; (316) 1. ii. 34.

CALADIUM BICOLOR (Ait). Vent.—Hog harbour, seen in the Government Agent's garden, but collected from bush; (356) 8. ii. 34.

CYPERACEAE.

MARISCUS CYPERINUS (Retz.) Vahl.—Hog harbour, Mission garden; (181, 182) 3. i. 34: Mt. Tabwemasana, open grassland, 4000 ft.; *Tabobauwe*; (2) 29. x. 33.

TORULINIUM FERAX (Rich). Urb.—Between Lowerie and Ladhogh, clearings; *Naradhiu*; (26) 27. xii. 33.

KYLLINGA MONOCEPHALA Rottb.—Hog harbour, Mission garden; (185) 13. i. 34.

CAREX NEOHEBRIDENSIS Guillaum. & Kükenth.—Mt. Tabwemasana, open grassland, 3000 ft.; grows 2 ft. high; (14) 4. xi. 33.

GRAMINEAE.

COIX LACRYMA-JOBII Linn.—Hog harbour, rain forest, 3 ft.; greyish fruit; *Nedhi*; (259) 25. i. 34.

IMPERATA EXALTATA Brongn.—Hog harbour, among gardens; copings of roofs made with this grass; (106) 21. xii. 33.

MISCANTHUS SINENSIS Anderss.—Hog harbour, rain forest; *Nedhur*; (294) 27. i. 34: clearings; children make the stalk into arrows to shoot small birds with; (319) 1. ii. 34: Mt. Linisupe, patches in clearings in mossy forest, 5000 ft., very common grass; 12 ft. high; (10) 1. xi. 33.

OPLISMENUS COMPOSITUS (Linn.). Beauv.—Hog harbour, rain forest; *Midhmidhara*; (93) 10. xii. 33.

ELEUSINE INDICA (Linn.) Gaertn.—Between Shark bay and Hog harbour; (167) 30. xii. 33.

PANICUM PRURIENS Fisch. ex Trin.—Hog harbour, Mission garden ; (184) 13. i. 34.

PASPALUM ORBICULARE Forst. f.—Hog harbour, Mission garden ; (183) 1. i. 34.

P. PANICULATUM Linn.—Hog harbour ; (45) 20. xi. 33 : Mission garden ; (186) 13. i. 34.

P. PANICULATUM Linn. ?—Hog harbour, rain forest ; Werü ; (306) 31. i. 34.

CYRTOCOCCUM TRIGONUM (Retz.) A. Camus (*Panicum trigonum* Retz.) *.—Hog harbour, rain forest ; (43) 20. xii. 33.

ISACHNE ALBENS Trin.—Mt. Tabwemasana, open grassland, 4,000 ft., common ; grows about 1 ft. high ; (12) 29. x. 33.

CENTHOTHECA LAPPEA (Linn.) Desv.—Between Salip and Shark bay, rain forest ; Midh-midh ; (147) 29. xii. 33 : Hog harbour, rain forest ; (44) 20. xi. 33.

GRAMINEA.—Hog harbour, rain forest ; *Ntasili* ; (46) 20. xi. 33.

ARAUCARIACEAE.

AGATHIS MACROPHYLLA (Lindl.) Mast. (*Dammara macrophylla* Lindl.).—North of Sara, very large tree, 30 feet in circumference, in rain forest, the only one of its kind in the district ; the bark is said to be very fattening when eaten, and resin is inflammable ; Numül ; (353) 8. ii. 34.

AGATHIS OBTUSA (Lindl.) Mast (*Dammara obtusa* Lindl.).—Hapuna Valley, mountain forest, about 2,000 ft. ; Kauri pine ; (360).

CYCADACEAE.

CYCAS CIRCINALIS Linn.—Hog harbour ; 27 ft. 6 in. high, 5 ft. circumference ; Nemol ; (30) ii. 34 : (199) 19. i. 34.

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* Determined by Mlle A. Camus,

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